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THE CLASSIFICATION OF THE TREMELLALES

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(WITH 1 FIGURE)

I

The classification of the Tremellales cannot be considered without reference to that of the Basidiomycetes as a whole, since the limits of the order, its presumed relationships with other orders and the interrelationships between its subdivisions are all parts of the larger problem. It seems desirable, therefore, to review briefly the varying concepts of the Basidiomycetes which have found more or less acceptance during the past two generations.

The treatment of the fungi in the earlier editions of Sachs's *Lehrbuch* (**27**) may be regarded as representing the viewpoint widely held at the beginning of the modern period. Sachs divided the fungi into four major groups, the Phycomycetes, the Hypodermiae (rusts and smuts), the Basidiomycetes and the Ascomycetes. In Goebel's adaptation of the Sachs text (**18**) the major groups were increased to six by the addition of the Chytridieae and the separation of the smuts and rusts, the former relegated to a place between the chytrids and the Phycomycetes; the latter put between the Ascomycetes and the Basidiomycetes. In both, the lichens are included in the Ascomycetes and the Myxomycetes are set apart from the other groups.

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In 1884, the German edition of de Bary's great work (**1**) appeared. De Bary, like Goebel, made the Uredineae a class coordinate with the Ascomycetes and Basidiomycetes and inserted between them. He placed the Ustilagineae with and after *Protomyces,* before the Ascomycetes, noting that he did not believe the smuts to be closely related to the rusts. He divided the Basidiomycetes into the Hymenomycetes and Gastromycetes. In connection with the former he stated: "In the simplest cases, such as . . . *Corticium, Dacryomyces, Exobasidium* and some species of *Hypochnus,* the compound sporophores do not vary essentially in form and differentiation from the layers of teleutospores in the Uredineae . . ." (**1**, p. 287). He regarded each cell of the divided basidia of *Auricularia* and *Exidia* as a separate basidium bearing a single spore.

De-Toni (**13**), in the first treatment of the smuts and rusts in the *Sylloge Fungorum,* referred to the asci in both groups. C. E. Bessey (**2**, p. 340) at first classed them with the Ascomycetes, but later (**3**) erected for them the class Teliosporae, coördinate with the Ascosporae and Basidiosporae. In this he was followed by Clements and Shear (**8**) and E. A. Bessey (**4**). The majority of other students writing since the beginning of the present century have recognized the smuts and rusts as Basidiomycetes. An obsolete terminology has persisted, however, which applies distinct names to structures in these fungi which appear to be entirely homologous with those designated by other terms in other Basidiomycetes, and this may have had more weight than is commonly realized in influencing their separation from certain of the Tremellales.

The classification of the Basidiomycetes which is most familiar at the present time reflects very largely the conclusions of Brefeld. In the first summary of his results, Brefeld (**6**, pp. 270–274) derived the smuts from the conidial Zygomycetes but did not include them in the Basidiomycetes, which he envisaged as having had an independent origin from the same source. The Basidiomycetes were divided into the Protobasidiomycetes, with septate basidia (Uredineen, Auricularieen, Tremellineen, Pilacreen), and the Autobasidiomycetes, with non-septate basidia. The Dacrymycetaceae and the Tulasnellaceae were included in this second

subclass with the thelephores, agarics and puffballs. In a subsequent volume (**7**, pp. 341–356), Brefeld recognized the smuts as a distinct class, the Hemibasidii, coördinate with the Ascomycetes and Basidiomycetes, and suggested that the Protobasidiomycetes had arisen from the Ustilaginaceae and the Autobasidiomycetes from the Tilletiaceae. Even while the later volumes of the *Untersuchungen* were appearing, cytological evidence was beginning to accumulate which was destined to destroy the foundations of the edifice which Brefeld had erected. Nevertheless, his system was adopted, with some modification, notably the unequivocal inclusion of the smuts in the Basidiomycetes as the class Hemibasidii, but with explicit adoption of his theory of the origin of basidia from conidiophores, by Lindau and Dietel in the first edition of Engler and Prantl. The wide popularity and extreme usefulness of that work quite naturally resulted in the acceptance of its classification by nearly all the textbooks and most of the systematic treatments published during the next third of a century. It remains the dominant treatment to-day.

An alternative classification, first outlined by Patouillard in 1887 (**23**) and greatly elaborated in his *Essai Taxonomique* of 1900 (**24**), proposed the division of the Basidiomycetes into two subclasses, the Hétérobasidiés, characterized by basidiospores which, in germination, habitually produce secondary spores and with basidia septate or deeply divided, and the Homobasidiés, bearing basidiospores which consistently germinate by the production of a mycelium and with cylindrical or clavate, undivided basidia. In the Hétérobasidiés, Patouillard recognized four families: the Auriculariaceae, with transversely septate basidia, in which he included the rusts and smuts, the Tremellaceae, with cruciate-septate basidia, the Tulasnellaceae and the Caloceraceae (*i.e.*, Dacrymycetaceae).

One great merit of Patouillard's arrangement is that instead of insisting upon rigid adherence to a single arbitrarily selected character he made his scheme elastic enough to permit the insertion of groups where they fit naturally on the basis of all characters taken together, as illustrated by his inclusion of the Tulasnellaceae and the Dacrymycetaceae in the Heterobasidiomycetes. Patouillard's own subsequent investigations did much to fortify his system, but

it was not until its adoption by Bourdot and Galzin in their notable series of papers on the Hymenomycetes that much attention was paid to it outside of France. The treatment of Coker (**9**) was in general accord with it, while its use by Rea in the British Basidiomycetes (**25**) and the publication of Bourdot and Galzin's great volume (**5**) compelled the mycological world to grant it respectful consideration.

Gäumann (**16**) divided the Basidiomycetes into Protobasidiomycetes, with the four orders Auriculariales, Uredinales, Ustilaginales and Tremellales, and Autobasidiomycetes, including the Tulasnellales and the Dacrymycetales in the latter groups. This is clearly based on Brefeld's system, somewhat modified and with emphasis on the chiasto-stichobasidial concepts of Maire and Juel. In Gäumann and Dodge (**17**) the treatment of the Basidiomycetes is radically altered. Starting with the Polyporales, in which are included, among others, the Tulasnellaceae and two rather dubious associated families, they follow them with the Agaricales, Cantharellales, Gasteromycetes, Dacrymycetales, Auriculariales, Uredinales and Ustilaginales, in the order named. Their treatment is admittedly influenced by the chiasto-stichobasidial theory so striking a feature of Gäumann's book, but in a foot-note (p. 413) Dodge recognizes that this has been overstressed.

In the second edition of Engler and Prantl (**6**: vii. 1928) the Basidiomycetes are divided into the subclasses Hemibasidii and Eubasidii. The Hemibasidii, by Dietel, includes the orders Ustilaginales and Uredinales, the two smut families separated as suborders, with reaffirmation of Brefeld's theory of the origin of basidia from conidiophores. The Eubasidii embraces the single order Hymenomycetae, with the Tremellineae, Hymenomycetineae and five Gasteromycete groups as suborders. In the special treatment of the Gasteromycetes by E. Fischer (**15**), however, the Gasteromycetes are ranked as an order, with six suborders. In his treatment of the Tremellineae, Killermann (**20**) recognizes three families, the Auriculariaceae, with the tribes Auricularieae and Phleogeneae, the Tremellaceae, with the tribes Sirobasidieae, Tremelleae and Hyalorieae, and the Dacrymycetaceae. In its recognition of the affinity of the Dacrymycetaceae with the groups possessing septate basidia, this is a definite advance over Brefeld's

classification. *Tulasnella* is included in the Tremelleae, where it could never be located by following the keys. Gwynne-Vaughan and Barnes (**19**) follow what is essentially Brefeld's system, including *Tulasnella* in the Thelephoraceae and merging the Dacrymycetaceae in the Clavariaceae. Bessey (**4**) adopts the name Heterobasidieae to include the orders Auriculariales, Tremellales and Dacrymycetales, excluding *Tulasnella,* with reservations, to the Thelephoraceae. Smith (**28**) divides the Basidiomycetes into the Eubasidii, with the orders Agaricales, Lycoperdales (including all Gasteromycetes), Dacrymycetales, Tremellales and Auriculariales, and the Hemibasidii, embracing the rusts and smuts.

It is evident that there is no general agreement either as to the basic division of the Basidiomycetes or as to the relative rank and limits of the various subdivisions. On the whole, the tendency in recent years has been to group the Dacrymycetaceae with the tremellaceous fungi and to recognize three orders of these fungi, based on the cruciate-septate, transversely septate and forked types of basidia. There has also been a tendency to emphasize the separation of the Auriculariaceae from the rusts by including these groups in different major subdivisions of the Basidiomycetes.

As has been stressed by Linder (**21**), the inadequate fossil record of the fungi compels us to base our ideas of their phylogeny upon evidence derived from the comparative study of living species, all of which have had abundant time in which to acquire modifications, and it is not easy to determine which characteristics resemble those of the hypothetical ancestral forms and which are of more recent origin. In the case of the lower Basidiomycetes, we have a more than usually complete series of transitional forms, constituting a network which may be traversed in almost any direction and in which, as in the peccary and tapir trails of a tropical forest, it is amazingly easy to become lost unless, before entering, one is careful to establish distinctive landmarks.

For the purposes of the present discussion, I shall adopt, as points of reference, the following postulates:

1. The fundamental character in the Basidiomycetes is the nature of the basidium, to which all other characters are subordinate.

2. It is to be expected that in all categories basic groups will, in general, be characterized by greater morphological simplicity and

flexibility than the more specialized and presumably derivative groups.

3. In derivative saprobic groups, the basidium tends to become stabilized and, in such groups, the organization of the basidiocarp becomes increasingly significant.

4. Adaptation to parasitic nutrition is an indication of relative specialization as compared with saprobism. It follows that parasitic forms may readily be conceived to have arisen from saprobic forms but that the reverse process is more difficult to explain.

With these as a guide, I shall attempt to defend the following theses:

I. That the primary division of the Basidiomycetes into Heterobasidiomycetes and Homobasidiomycetes, as proposed by Patouillard, furnishes the best basis for a natural system which has thus far been suggested.

II. That within the Heterobasidiomycetes, three, or at most four orders should be recognized: the Tremellales, Uredinales, Ustilaginales and possibly the Septobasidiales, and that within the Tremellales, in the inclusive sense, the transitions between the various types of basidia are such as to make untenable the maintenance of the Auriculariales and Dacrymycetales as distinct orders.

III. That the Tremellales, more than either the Uredinales or Ustilaginales, retains the largest number of primitive characters and that within its limits, as here defined, there exist forms which afford a satisfactory transition to the rusts, on the one hand, and to the Homobasidiomycetes, on the other.

All modern systems which separate the smuts, as Hemibasidiomycetes, from all other Basidiomycetes are, as stated, based on Brefeld's theory of the origin of basidia from conidiophores. No additional reasons have been advanced for this disposition of the group and with the collapse of the theory on which it was based the only reasons for continuing to employ it are inertia and adherence to tradition.

The systems which place the rusts and smuts together but separate them from the rest of the Basidiomycetes are more defensible, since there is much reason to suppose that these two orders may be closely related, but they are defective in their failure to give

adequate recognition to the many similarities between the rusts and certain of the auriculariaceous genera. Even if, as Linder and others suppose, the rusts constitute the basic basidiomycete order from which other Basidiomycetes have been derived, this criticism is still valid.

The systems which include the rusts and smuts together with those tremellaceous fungi with cruciate-septate or transversely septate basidia in a single series, but relegate the Dacrymycetaceae and Tulasnellaceae to another series as homobasidiate fungi, are, in the case of the Dacrymycetaceae, stressing a single character to the exclusion of numerous others which point to the heterobasidial nature of the family, and, in the case of the Tulasnellaceae, substituting a far-fetched and wildly improbable theory of the nature of the tulasnellaceous basidium for a simple and obvious one.

As compared with these schemes, and on the basis of known living representatives, the concept of the Heterobasidiomycetes and Homobasidiomycetes as representing two parallel series, very close together—scarcely separable in fact—at the hypothetical bases, but each developing in its own distinctive fashion quite independently of the other, fits the known facts far more accurately.

II

For the purposes of the present discussion, it may be assumed that the great majority of mycologists are content to recognize the adequacy of according ordinal rank to the Uredinales and Ustilaginales. But, as has been noted, there has been great difference of opinion as to the arrangement and rank of the remaining groups. To support the thesis that they may all be included in a single order, it is necessary only to demonstrate that the different types of basidia are more variable and that the intergradations between these types are more frequent than has commonly been supposed. Without, at this time, considering any phyletic implications, it may be profitable to start with *Ceratobasidium,* certainly a genus in which most of the few known species are among the morphologically simplest of the Basidiomycetes. The loose weft of hyphae which suggests rather than constitutes a basidiocarp; the short, thick basidia with their swollen epibasidia, borne in waxy tufts; the germination of the basidiospores by repetition—all combine to

create a strong suggestion of primitiveness. As noted by Linder, the resemblance of *Ceratobasidium* to the species of *Pellicularia* (*Botryobasidium*) makes it possible to connect the genus with the whole series of Homobasidiomycetes. On the other hand, aside from the fact that the epibasidia are not cut off from the hypobasidium by septa, they are in every respect so like the Tulasnellas that in a recent treatment (**22**) I have felt justified in including them in the Tulasnellaceae. Again, in *Ceratobasidium sterigmaticum* we have so close an approach to the Dacrymycetaceae, as represented by *Ceracea crustulina,* that placing the two species in distinct families can be justified only on the ground that, despite the recognized similarities at this level, the Dacrymycetaceae does constitute, on the whole, a compact and homogeneous group of genera representing one line of development, not, however, to be separated by more than a family line from other groups which can be connected with the same center.

The differences between the *Tulasnella* basidium and the cruciate-septate type, while very real, should not be over-emphasized. In the tenuous and more arid Sebacinas the basidia may be as widely scattered as in any *Tulasnella* or *Ceratobasidium,* and in some of these the epibasidia may be entirely lacking, each segment of the mature basidium giving rise directly to a sterigma and a spore. In such basidia there may be a marked tendency for the basidial cells to separate at maturity. But in most cases the epibasidia are well developed and in the soft and highly gelatinized large Tremellas, represented by *T. mesenterica,* they are enormously thickened at the apex, terminating in a bulbous tip which supports a sharply differentiated sterigma. When to this is added the presence of an empty, basal stalk-cell, cut off in basidial development, and the strongly lobed and often nearly separate divisions characteristic of *Protohydnum* and certain species of *Sebacina,* the resemblance to *Tulasnella* is not entirely fanciful.

Irregularities in number and orientation of septa are common in many tremellaceous fungi with cruciate-septate basidia and these sometimes approach remarkably closely to the transversely septate type. We are not, however, dependent upon these abnormalities to make the transition to the Auriculariaceae. In the genus *Patouillardina* the probasidia are elongate-fusiform, the primary

septum is regularly transversely oblique and the secondary septa are at right angles to it, usually reaching it, but not infrequently extending to the basidial wall, each cell so formed sending out a tortuous epibasidium to the surface of the waxy-gelatinous hymenium, and the whole structure, except for the orientation of the septa, remarkably like a *Platygloea* or an *Auricularia* basidium.

In *Auricularia* the probasidium as a whole is divided by transverse septa into four equal portions, fundamentally as in *Patouillardina,* each portion sending out a single tortuous epibasidium to the surface, where again definitive sterigmata are produced. Through *Platygloea* there is transition to *Helicogloea,* with its peculiar saccate probasidium, and, presumably independently, to the as yet unnamed species of *Herpobasidium* on *Lonicera* and to *Eocronartium, Jola* and *Cystobasidium,* all with definite and, in the last-named genus, somewhat thick-walled probasidia, strongly suggestive of the teliospores of rusts. Significantly associated with this resemblance is the parasitic habit characteristic of the species belonging to these genera.

The *Phleogena* basidium and spores have little in common with those of the other transversely septate groups and the associated genera in the Phleogenaceae are too little known to justify much speculation as to relationships with other groups, but it would not be surprising if further study of *Pilacrella* and similar genera were to indicate that *Phleogena* represents the terminus of its own developmental line.

Septobasidium deserves very special consideration. The curious symbiotic-parasitic relation with scale insects, almost exactly paralleling that of the lichen fungi with their host algae and resulting in a suggestively similar thallus, has led Couch (**11**), to whose researches we are indebted for the great bulk of our knowledge of the genus, to claim for it ordinal rank. Opposed to this conclusion, however, is the almost complete gradation of the probasidia from those in which they are scarcely more specialized than in *Auricularia,* through forms with a thin-walled but persistent hypobasidium to those in which the probasidium closely resembles a rust teliospore and functions like one. The relationship of the genus with the rusts is further emphasized by the existence of *S. Polypodii* Couch, which was later assigned to the rusts by

its author, principally because it does not parasitize scale insects, and the curious genus *Uredinella* Couch (**10, 12**), distinctly intermediate between the two groups.

The small families Sirobasidiaceae and Hyaloriaceae need not be discussed at length. The catenulate basidia of *Sirobasidium* are not rarely matched in *Gloeotulasnella pinicola* and may occasionally be observed in several species of *Tulasnella*. The lack of epibasidia and sterigmata is more significant. It may be that the spores are really homologous with epibasidia or perhaps the suppression of sterigmata represents a response on the part of immersed basidia analogous to that which has resulted in the sessile spores of certain Gasteromycetes. The latter comment might be applied in a slightly different sense to *Hyaloria*, in which the basidiospores are borne on slender stalks which are neither epibasidia nor functional sterigmata, but more like the stilt-like structures found in the Lycoperdaceae, and, like them, display a tendency to break some distance below the spores. Aside from this peculiarity, there is little to separate *Hyaloria* from the Tremellaceae. In any event, no one has seriously suggested that either of these families deserves elevation to the rank of an order.

III

I have already suggested that morphological simplicity, flexibility of expression of characters and a saprobic habit may be interpreted as indicating primitive position among these fungi as contrasted with morphological complexity, relative stability of characters and a parasitic habit. To these might be added germination by repetition as contrasted with germination by a mycelial tube, despite the fact that it is widespread among the Heterobasidiomycetes as a whole. It is, of course, recognized that an organism may be primitive in some respects and advanced in others.

The lack of a highly developed basidiocarp in the Heterobasidiomycetes as compared with the Homobasidiomycetes and the slight economic importance of the mainly saprobic Tremellales as compared with that of the rusts and smuts are doubtless largely responsible for the fact that the classification of the Tremellales has lagged so far behind that of the groups named. Most of the species of Tremellales are resupinate and the most elaborately or-

ganized *Tremella* or *Dacryomitra, Phlogiotis* or *Phleogena* is no more complicated than a *Stereum* or a *Clavaria* and far below the organizational level of the hemiangiocarpous boletes or agarics, to say nothing of the phalloids and most of the other Gasteromycetes. On the other hand, the basidia in the Heterobasidiomycetes as a whole as in individual species of the group are much more variable than in the Homobasidiomycetes.

Linder regards the pustulate fructification as more primitive than the resupinate and cites this as evidence of the basic character of the rusts. But a pustulate origin of resupinates is extremely common and is well illustrated by species of *Tulasnella, Arrhytidia* and *Sebacina.* In *Stypella* and in several of the minute species of *Tremella* the fully mature basidiocarps remain pustulate. The distinction seems to be of subordinate importance.

The basidia of certain of the Heterobasidiomycetes are notoriously variable both in number of spores produced and in septation. Coker (**9**) has illustrated a number of such variations in the Tremellales. By careful observation of the basidia of a series of fructifications belonging to almost any of the species it is easy to duplicate basidia such as he has shown and to add others. Brefeld speaks scornfully of Tulasne's illustration of the basidia of *Phlogiotis Helvelloides* in which they are shown as 2-celled, but it is possible to find fructifications of that species in which practically all basidia are 2-celled, although 4-celled basidia predominate in most collections. Reference has already been made to the variation in *Patouillardina,* in which some of the basidia in almost any mount will approach those of *Auricularia.* I have illustrated comparable irregularities in *Coleosporium,* generally regarded as a primitive rust. Many other instances could be adduced. It is, of course, true that similar aberrations may sometimes be observed in Homobasidiomycetes, but they are far less common and are usually associated with some environmental disturbance, such as exposure to cold while the basidia are maturing.

If the parasitic habit in Basidiomycetes is primitive and the saprobic habit derived, then, as Rogers (**26**) points out, the transition from parasitism to saprobism must have occurred many times and independently. Linder finds this easy to believe. I agree with Rogers in considering the reverse process much more

comprehensible, particularly when large and morphologically coherent groups of species are uniformly parasitic. This is not to deny that occasional reversals may have occurred, but such reversals would be expected, if anywhere, among the relatively unspecialized parasites capable of attacking a wide range of hosts and of living for long periods saprobically. In the series which I should assume ends rather than begins with the rusts, the transition from saprobic genera through such weak or occasional parasites as may be found in *Auricularia, Cystobasidium* and *Helicobasidium* to strong parasites such as *Herpobasidium, Eocronartium* and *Jola* leads by very close stages to *Septobasidium* and the rusts. The rusts, as a whole, comprise a highly specialized group, evidenced by their striking adaptation to limited host ranges and by the complicated life cycles which are particularly characteristic of what are regarded as the more primitive representatives of the order.

In general, the development of a parasitic habit is associated with the presence of a vesicular probasidium, serving as a storage organ until conditions are favorable for the formation of the spore-bearing outgrowth or epibasidium. Sometimes this is thin-walled, as in *Eocronartium, Jola* and *Herpobasidium;* sometimes the walls are slightly thickened, as in *Cystobasidium;* sometimes definitely thick-walled, as in many species of *Septobasidium.* The structure reaches its climax in the rusts, where the thick-walled probasidia may be borne singly or grouped in characteristic clusters of fixed form, constituting the compound teliospores. In this feature, as in others, there are some exceptions. All variations occur in *Septobasidium,* and a well-developed hypobasidium is found in *Helicogloea,* in at least one species of *Platygloea* and in *Neotyphula,* all of which are, so far as known, saprobic.

Germination by repetition is characteristic not only of the great majority of the Heterobasidiomycetes, including the rusts and smuts, but also of a limited number of the lowest Homobasidiomycetes. In many species of the Tremellaceae it exists side by side with the capacity to form blastospores or conidia. Only in the Dacrymycetaceae does it seem to have been completely replaced by the latter method. These facts justify us in regarding it as a primitive character which has been retained by advanced

Heterobasidiomycetes but discarded by all but a few Homobasidiomycetes.

In the Tremellales we find a striking preponderance of those features—relative simplicity of basidiocarp, heterogeneity of basidia, saprobism, germination by repetition—which may be taken as indications of a primitive position among the Basidiomycetes. Within the Tremellales, the considerations which may be advanced for regarding the *Tulasnella* basidium as representative of a basic type have been clearly stated by Rogers (**26**). Without repeating his arguments, except insofar as much of the present discussion must inevitably reflect them, it may be said that the not inconsiderable addition to our knowledge of the lower Basidiomycetes which has been made during the decade since his paper appeared has strengthened the position there upheld, modifying it in some respects, clarifying it in others. From the Tulasnellaceae as a center we may trace four almost complete series, three of them leading directly or indirectly to other families of the order and through the Auriculariaceae to the rusts and, less clearly but highly probably, to the smuts, and the fourth to such morphologically simple and hypothetically primitive thelephores as *Pellicularia* and thence to other members of the *Corticium*-complex and the remaining Homobasidiomycetes. Such a picture agrees with the known facts and makes more adequate provision for the transitional forms than the systems which are in current use. Its greatest weakness is its failure to point to any close and convincing connection with the Ascomycetes. In view of the large number of species of Basidiomycetes and the wide geographical distribution of many of them, it seems highly probable that the class is very ancient and that the development of the basidium took place in the remote past. Even so, the discovery during the past half century of so many significant connecting links within the Tremellales permits us to hope that we may eventually secure clearer evidence concerning their source than has yet been presented.

The accompanying chart (FIG. 1) attempts to present in graphic form the relationships I have suggested. The genera named are those through which transition to a neighboring family is suggested. They are all sufficiently well known to give reasonable

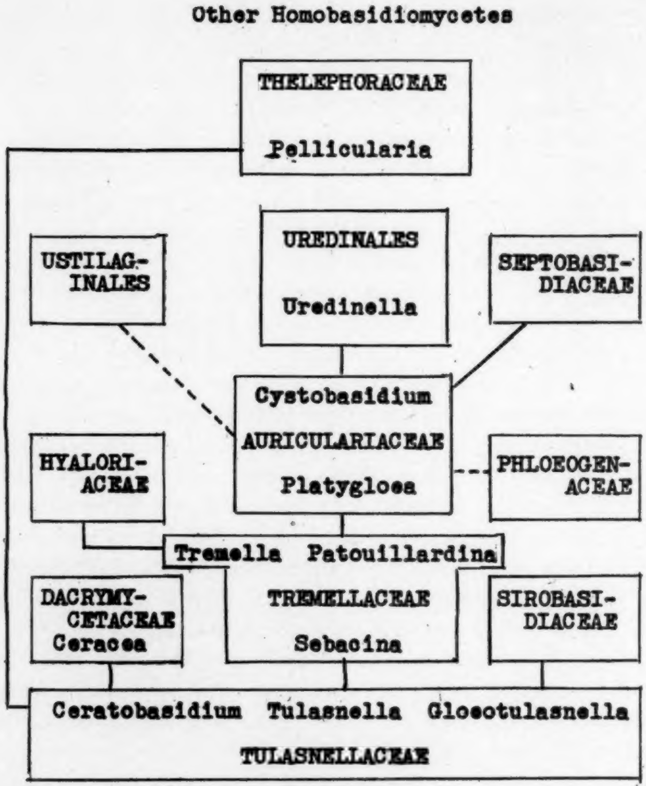

FIG. 1.

assurance that the interpretation of their morphology is correct. It seems clear that the reality of these transitions must, in most cases at least, be recognized. It is true that a connected scheme of this sort remains connected no matter which group is placed at the bottom. Linder has presented the case for starting with the rusts. I have presented the case for the only reasonable and, in my opinion, the preferable alternative. Whether it be accepted or rejected, this discussion will have served its purpose if it leads to greater interest in the reclassification of the Basidiomycetes.

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A NEW DACRYMYCES-LIKE PARASITE OF ARUNDINARIA

LINDSAY S. OLIVE[1]

(WITH 35 FIGURES)

Recently, an unusual *Dacrymyces*-like fungus, parasitic on the leaves of *Arundinaria tecta* (Walt.) Muhl., was received by the Division of Mycology from the Bureau of Entomology and Plant Quarantine. Mr. John A. Stevenson, recognizing the unique nature of the fungus, turned over to the writer two collections of it which he had received. Both specimens were collected in November of 1943, one at Savannah, Georgia, and the other at Aurora, North Carolina.

On looking over the list of fungi reported on *Arundinaria tecta* in Seymour's Host Index, the writer found the name of *Dacrymyces epiphyllus* Schw. listed among the parasites of this plant. A check-up on the report has disclosed several interesting facts. In 1832, Schweinitz (Syn. Fung. Am. Bor., No. 1130, p. 186) applied the name, *Dacrymyces epiphyllus,* to a fungus which he believed to be parasitic on the leaves of *Galium.* A study of a portion of the type collection of Schweinitz' fungus in the Mycological Collections of the Bureau of Plant Industry has shown that the host is not *Galium,* but *Euthamia graminifolia* (L.) Nutt. The writer has found, upon further investigation, that the parasite is not a *Dacrymyces,* but is the telial stage of *Coleosporium delicatulum* (Arth. & Kern) Hedgc. & Long. The little yellow, gelatinous, telial pustules had been mistaken by Schweinitz for a *Dacrymyces.*

This finding made it obvious that the report of *Dacrymyces epiphyllus* on *Arundinaria tecta* was also a mistake. Through the kindness of Dr. David H. Linder, we were able to obtain from the Farlow Herbarium Index the source of this report. In a list of

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Alabama fungi compiled in 1897 by G. F. Atkinson (1), the following note was found: "*Dacryomyces epiphyllus?* On leaves of *Arundinaria tecta.* Auburn *2327,* Nov. 3, 1891." The question mark indicated Atkinson's uncertainty about the validity of his identification. This same report occurred again, without the question mark, in Mohr's *Plant Life of Alabama* (Contrib. U. S. Nat. Mus. **6**: 196. 1901).

At the writer's request, Dr. H. M. Fitzpatrick sent from the Mycological Collections at Cornell University a portion of what appears to be Atkinson's only collection of this fungus on *Arundinaria tecta.* The parasite proved to be identical with the one described here. Investigations have shown that the fungus possesses certain characteristics which clearly indicate that it belongs in the Dacrymycetaceae. However, it is equally obvious that the organism is quite distinct from any other genus in that family. It is here described as a new genus and a new species.

Dicellomyces gen. nov.

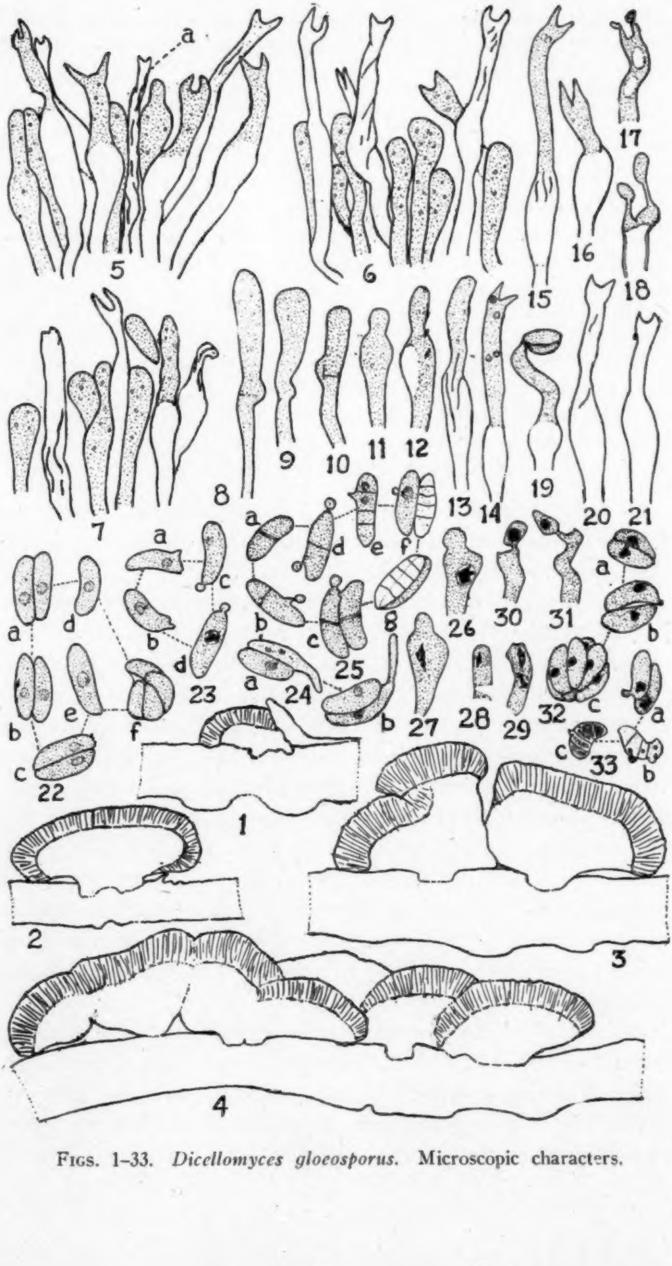
Fructificationes in foliis parasiticae, parvae, flavae, firme gelatinosae, pulvinatae usque subdisciformes, in textura folii basi obtusa insertae; basidia e probasidiis tenuibus persistentibus oriunda, extra superficiem fructificationis producta; sterigmata dua, comparative brevia; basidiosporae allantoideae, demum septatae, sporidia parva, globosa gerentes.

Type species *D. gloeosporus.*

Leaf parasite; small, yellow, firmly gelatinous, pulvinate to nearly discoid, with a blunt base inserted into the leaf tissue; basidia arising from thin-walled, persistent probasidia and produced externally to the surface of the fructification; sterigmata 2, becoming septate, producing small, globose conidia.

Dicellomyces gloeosporus sp. nov.

Fructificationes hypophyllae in maculis decoloribus, parvae, flavae, firme gelatinosae, pulvinatae usque subdisciformes, in substrato basi obtusa insertae, hyphis in folium penetrantibus, 440–700 × 485–955 μ, 194–353 μ altae, in aetate nigrobrunnescentes et collapsae; hymenium superficiem superiorem totam fructificationis tegens, e probasidiis 4.1–6.3 μ in diam., dense compactis, longe pedicellatis, clavatis vel subpyriformibus basidia gerentibus compositum; basidia angusta, in longitudinem variabilia, 2.4–4.1 × 9–25.2 μ, extra superficiem gelatinosam producta, sterigmata dua, comparative brevia, 1.8–4.0 μ longa gerentia; basidiosporae allantoideae, 2.7–4.5 × 8.6–11.9 μ, in paribus



FIGS. 1–33. *Dicellomyces gloeosporus.* Microscopic characters.

adhaerentibus productae, paribus pluribus saepe in globulam conglutinosis, apiculo non evidente, frequenter 1–4-septatae, saepe gemmantes et sporidia parva, subglobosa gignentes.

In foliis *Arundinariae tectae*.

Fructifications hypophyllous, on discolored spots, small, yellow, firmly gelatinous, pulvinate to nearly discoid, with a blunt base inserted in the leaf, hyphae penetrating into the leaf tissue, measuring 440–700 × 485–955 μ and 194–353 μ tall, becoming dark brown and shrunken with age; hymenium covering entire upper surface of the fructification, composed of closely packed, long-stalked, clavate to nearly pyriform probasidia, 4.1–6.3 μ in diameter, the latter persistent and giving rise to narrow basidia of varying lengths; basidia 2.4–4.1 × 9–25.2 μ, produced externally to the gelatinous surface, giving rise to 2 relatively short sterigmata, 1.8–4.0 μ in length; basidiospores allantoid, 2.7–4.5 × 8.6–11.9 μ, produced in adherent pairs, several pairs often clinging together in a ball, apiculus not apparent, basidiospores frequently becoming 1–4-septate, often budding out small, more or less globose, conidia.

On leaves of *Arundinaria tecta* (Walt.) Muhl., Savannah, Georgia, November 9, 1943, A. W. Blizzard, **type**; Aurora, North Carolina, November 12, 1943, C. S. Tuthill.

The first symptoms of the parasite on its host are the appearance of small yellow spots on the leaves. These spots enlarge and become dark brown, usually with a surrounding yellow area. The small yellow fructifications can be seen on these discolored areas. Eventually, large portions of badly diseased leaves may become brownish and dead. The spots show up with about equal clarity on both surfaces of the leaf. In figure 34, the upper surface of the first two leaves (*a* and *b*) and the lower surface of the third leaf (*c*) are shown.

The fructifications appear only on the lower surface of the leaves and look much like a minute *Dacrymyces* (FIG. 35). These sporocarps are bright yellow when dry, but become a lighter shade of yellow on being soaked. There is about a 30–50 per cent expansion when they are placed in water.

The fructifications arise singly or in groups which often anastomose (FIGS. 1–4, 34, b). The young sporocarp arises from within the leaf and, as it enlarges, ruptures the overlying epidermis (FIG. 1). Transverse sections of the leaf in the diseased areas show that the sporocarp is attached within the leaf by a blunt base.

These sections also show that the fructification is composed of an inner sterile tissue and an outer hymenial layer which covers most of the exposed surface (FIGS. 1–4).

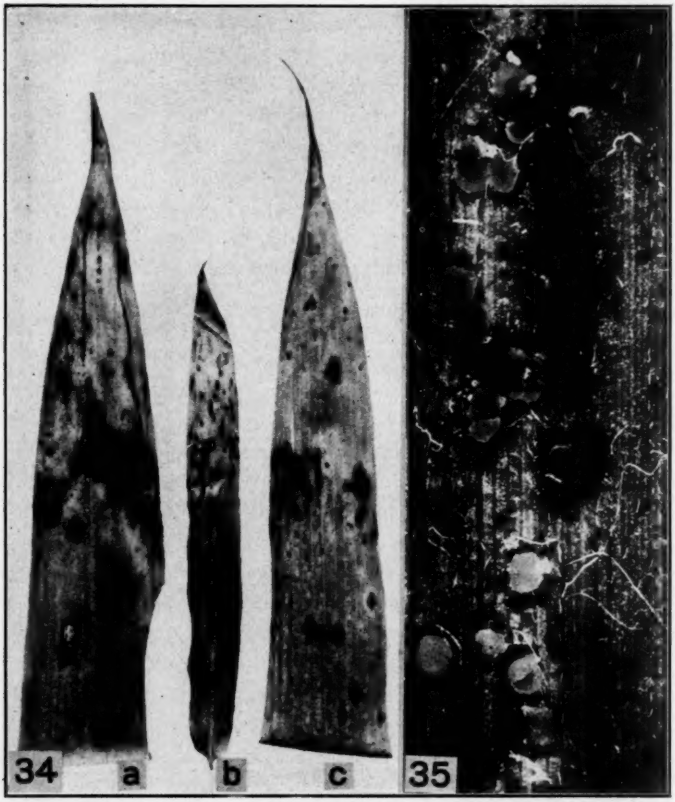
The structure of the hymenial layer appears to be different from that described for any other member of the Dacrymycetaceae. The hymenium is composed entirely of long-stalked, clavate to nearly pyriform probasidia embedded in the gelatinous substance of the fructification. Sometimes clamp-like processes were seen at the bases of the probasidia (FIGS. 8–10), but such structures were generally difficult to make out in this material. The probasidia, upon germinating, produce narrow basidia of varying lengths which come to lie entirely outside the gelatinous surface (FIGS. 5–7). The probasidia empty all their protoplasmic contents into the basidia and remain distinct for some time afterwards (FIGS. 5–21).

The mature basidium is terminated by 2 sterigmata which are decidedly shorter than those of any other fungus described for this family. Of course, these sterigmata do not have to perform entirely the same functions as the longer ones of other Dacrymycetaceae; that is, they do not have to extend through a gelatinous layer in order to bring the basidiospores to the surface. Each basidium produces two basidiospores, which, as they enlarge at the tips of the sterigmata, come together along their inner surfaces and adhere (FIGS. 17–19). They are always shed in adherent pairs (FIGS. 22, *a, b, c;* 32, *a, b*), or several approximate pairs may cling together in agglutinated balls (FIGS. 22, *f;* 32, *c*). They are probably not discharged forcibly from the sterigmata. Although these spores are rather strongly adherent, some of them eventually become separated, as many of the figures show. They are allantoid in shape and without apiculi. After sporulation, basidial and probasidial walls may remain expanded, but eventually they both collapse (FIGS. 5*a*, 7).

Most of the material examined was mounted in a phloxine preparation, after which nuclei could generally be made out within the basidiospores. The spores are at first uninucleate. Later they become septate and multinucleate. While they are unicellular, they may bud out tiny globose conidia (FIG. 23), or they may sometimes produce slender germ tubes (FIG. 24). Frequently

they become 1–4-septate and bud out conidia in a manner typical of *Dacrymyces* (FIG. 25).

Although none of the material used in the present investigation was alive, some of it was carried through a nuclear staining



FIGS. 34, 35. *Dicellomyces gloeosporus* on leaves of *Arundinaria tecta*.

technique as for live material. A few pieces of a diseased leaf containing some of the fructifications were placed in chromic-acetic-osmic acid solution. Later they were imbedded in paraffin and sectioned, and the sections were stained with the iron-alum haematoxylin procedure. Conclusions based on a study of such

material must, of course, be made with caution, since nuclear phenomena are easily confused with numerous artifacts which are generally present. However, a few important details were obtained from a study of this material.

The main purpose of this cytological investigation was to determine the orientation of the spindles during meiosis. Indications are that the first division is in progress before the nucleus has passed from the probasidium into the developing basidium (FIGS. 26, 27), and that there is a second division in the basidium (FIGS. 28, 29). The few spindles observed seemed to be parallel to the long axis of the basidium. Thus it appears that the fungus is truly phragmobasidial in nature, as one might have expected from its obvious relationship to other Dacrymycetaceae.

More clearly in evidence than any other cytological detail was the uninucleate condition of the basidiospores (FIG. 32). Each spore receives a single nucleus when it is produced (FIGS. 30, 31). A few spores, unicellular and septate ones, were observed producing conidia (FIG. 33).

The important characteristics of *Dicellomyces* which seem to justify its being considered a new genus of the Dacrymycetaceae, distinct from all other genera of that family, may be summarized as follows: (1) its parasitic nature on a seed plant, (2) the presence of persistent probasidia, (3) basidia produced externally to the gelatinous hymenium, and (4) relatively short sterigmata. The fungus is placed in the Dacrymycetaceae on the basis of (1) its characteristic yellow, firmly gelatinous sporocarps, (2) 2-sterigmate basidia, (3) phragmobasidial nature, and (4) basidiospores which may become septate and which may bud out small, globose conidia.

The present fungus seems to exhibit several interesting similarities to and parallelisms with other groups of fungi. The development of a slender, 2-sterigmate basidium from a persistent probasidium and the parasitic nature of the fungus are characteristics which are found in *Brachybasidium Pinangae* (Rac.) Gäum. The fruiting bodies of the latter appear as numerous small, hemispherical bodies which emerge from the stomata on the underside of *Pinanga* leaves. They appear to consist entirely of a few probasidia which give rise to slender 2-sterigmate basidia in a manner

similar to that described for the present fungus. Although no reference was found concerning the texture of these fructifications, either in Raciborski's (**4**) original description of the fungus, or in Gäumann's (**2**) later treatment of it, the present writer finds that the probasidia seem to be held together by a gelatinous substance, which is more in evidence when some of the material is soaked in water. Apparently, the only outstanding morphological difference between the fructification of *Brachybasidium* and that of *Dicellomyces* is the absence of the sterile sub-hymenial tissue in the former.

On the other hand, Gäumann (**2**) has shown, in a limited cytological investigation of *Brachybasidium Pinangae,* that the meiotic spindles in the developing basidium are at right angles to the long axis of the basidium. This chiastobasidial nature of the fungus and the presence of a *Dacrymyces*-like basidium arising from a distinct and persistent probasidium make a peculiar combination. However, Gäumann mentions several times in his discussion the difficulty which he experienced in trying to obtain material with clear cytological details, and it may be that his figures were misinterpreted on this account. The later development of the basidiospores after they are shed is not described.

If *Brachybasidium* should prove definitely to be chiastobasidial, it is not likely that the fungus can be considered closely related to *Dicellomyces.* On the other hand, if it should prove to be phragmobasidial in nature, only a reduction in the size of the *Dicellomyces* type of fructification would be required to derive that of *Brachybasidium.*

From the standpoint of its parasitic nature and persistent probasidia, *Dicellomyces* appears to occupy a position in the Dacrymycetaceae similar to that held by such genera in the Auriculariaceae as *Iola* and *Herpobasidium,* which are also parasitic on higher plants and have persistent probasidia. Since both families are composed primarily of saprophytic fungi, which generally have no distinct resting phase in the development of the basidium from the probasidium, the combination of these two characters is exceptional. From the standpoint of phylogeny in these two families, such forms are of the greatest importance. They emphasize the probability of the origin of these groups from

rust-like ancestors. The present fungus must have had its origin either in a rust-like ancestor which possessed persistent probasidia, or from a parasitic ancestor which had inherent within it the tendency to produce resting probasidia and from which other heterobasidiomycetes, including the rusts, might also have evolved.

In the light of the above discussion, it would seem less likely that the *Dacrymyces* type of basidium can be derived from the *Corticium sterigmaticum* type, as Rogers (**5**) has suggested. Moreover, it would appear that the latter's consideration of the resupinate *Ceracea* type of fructification as the most primitive in the Dacrymycetaceae is no longer well founded. On the other hand, the present investigations tend to add support to the theory held by Linder (**3**) that the Dacrymycetaceae were evolved from rust-like ancestors and that the pustulate fructification preceded the resupinate in the evolutionary development of the group. The present writer would not, however, entirely eliminate the possibility of an origin from a rust-like ancestor which already possessed resting probasidia. Linder's selection of the *Coleosporium*-like ancestor for his starting point in the derivation of the dacrymycetaceous line does not permit this possibility, but at the same time does not preclude the possibility that a derived form may have inherited the tendency towards the production of persistent probasidia.

SUMMARY

1. A leaf parasite of *Arundinaria tecta*, representing a new genus and species, has been described. The name *Dicellomyces gloeosporus* is proposed.

2. The fungus resembles *Dacrymyces* in its color, form of fructification, gelatinous nature, 2-sterigmate basidia, and allantoid basidiospores which may become septate and which frequently bud out globose conidia.

3. It differs from all other genera of the Dacrymycetaceae in its persistent probasidia, basidia produced externally to the gelatinous matrix, and relatively short sterigmata.

4. The parasitic and phragmobasidial nature of the fungus and its possession of persistent probasidia are believed to be primitive

characteristics which point toward the origin of the group from rust-like ancestors.

The author is grateful to Miss Edith Cash for her preparation of the Latin diagnosis, and to Dr. C. L. Lefebvre, of the Forage Crops Division, for the use of his staining facilities. The author also appreciates the assistance of Dr. Charles Drechsler in helping him select an appropriate name for the fungus.

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EXPLANATION OF FIGURES

FIGS. 1–33 (All figures × 945, except 1–4, × 66). Microscopic characters. 1, Young fructification breaking through lower epidermis of leaf of *Arundinaria tecta,* hymenium represented by striations; 2–4, fructifications on lower surface of leaf, some anastomosing; 5–7, details of the hymenium, showing probasidia and basidia, *a,* collapsed basidium and probasidium; 8–10, probasidia with clamp-like processes; 11–16, development of the basidia (Note the emptying of the probasidia); 17–19, development of the basidiospores, figure 19 showing 2 agglutinated spores; 20 and 21, empty probasidia and basidia; 22, basidiospores, *a, b, c,* typical agglutinated pairs, *c, d,* single spores, *f,* agglutinated ball of spores; 23, unicellular basidiospores producing conidia; 24, basidiospores producing germ tubes; 25, septate basidiospores, some producing conidia; 26–33, cytological details: 26 and 27, beginning of first meiotic division in the probasidia; 28 and 29, second meiotic division in the young basidia (Note orientation of spindles); 30 and 31, development of uninucleate basidiospores; 32, uninculeate basidiospores, *a* and *b,* typical agglutinated pairs, *c,* agglutinated ball of spores; 33, basidiospores producing conidia.

FIGS. 34, 35. Appearance of fungus on the host. 34, Leaves of *Arundinaria tecta,* showing leaf spots caused by the fungus, *a* and *b,* upper leaf surface, *c,* lower surface, natural size; 35, appearance of the fructifications on the lower surface of the leaf in moistened material, × 10.

THE SIGNIFICANCE OF ZYGOSPORE CHARACTER IN POLYPHAGUS EUGLENAE

A. F. BARTSCH

(WITH 23 FIGURES)

Polyphagus Euglenae Nowak. is perhaps one of the most intensively studied species of the aquatic Chytridiales and has been known since the early collection by Gros (**1851**) who was unaware of the true nature of the organism which he described and figured. It has been reported since that time from all parts of Europe, from Asia and the United States and perhaps is cosmopolitan at least in the northern hemisphere. The life history of this form is quite completely known from the excellent and intensive researches of Nowakowski (**1876**, **78**), and knowledge of its cytological and morphological development has been supplied by Dangeard (**1900–01**) and by Wager (**1898**, **1899**, **1913**). In spite of this intensive investigation into the details involved in the parasitism, growth and sexual and asexual modes of reproduction, controversies have arisen concerning some of the fundamental points involved in the life history. Some of these relate to the phototactic nature of the zoospores (Wager, **1913**), the function of sexually differentiated zoospores in determining the development of an incipient thallus into a functional male or female gametangium (Kniep, **1928**), the significance of the formation of two kinds of zygospores which differ primarily in possessing or lacking an ornamented exospore (Nowakowski, **1876**, **78**; Dangeard, **1900–01**; Wager, **1913**; Sparrow, **1936**, **43**), and the validity of reports of the occurrence of two distinctly different processes in the formation of the zygospores (Nowakowski, **1876**, **78**; Wager, **1913**; Dangeard, **1900–01**). The present study is concerned primarily with the relationship of the two kinds of zygospores found in this fungus and with the methods involved in their formation.

Occasionally there have appeared in mycological literature reports of finding two kinds of zygospores in *P. Euglenae*. These spores are reported to differ from each other mainly in the possession of a smooth exospore in the one type and a spiny one in the other. In the accounts of early collection and culture of this fungus, the presence of both types led to speculation concerning their relationship. The fact that all vegetative thalli were more or less similar in all apparent respects led some to believe that the zygospore differences are not of specific significance and that whatever differences were found in the vegetative thalli represented the anatomical variation between specimens within the species. This apparently is the view held by Nowakowski in 1876 because he suggested that the ornamented type is normal and that the smooth type is the result of abnormal development under poor nutritional conditions. He also reported that the smooth form is produced as the result of communication by the tip of a male conjugation tube with the already extruded contents of a female thallus. In addition, he suggested that it may be formed as the normal zygospore of a distinct "race" of *P. Euglenae*. Two years later (**1878**), however, and after additional study of the smooth type, he stated that his previous report on the method of smooth zygospore formation is erroneous and based upon the study of an insufficient number of specimens. He concluded, in addition, that the fungus is distinct from the spiny form and described it under the trinomial, *P. Euglenae* var. *minor*. This was done on the basis of the smaller size of the vegetative thalli and apparently on the assumption that the smooth character of the zygospore wall is constant. There is no evidence that this conclusion was based upon the observation of unifungal cultures through a number of generations although he (**1878**) refers to its collection in a street gutter at Lwów as if it occurred there by itself.

Dangeard (**1900–01**) also found both types of zygospores in his cultures and, apparently unaware of Nowakowski's later paper (**1878**), adopted his earlier view that the wall differences are the result of nutritional influences. Wager (**1913**), in studying the cytology of *P. Euglenae*, was inclined to agree with Dangeard. Sparrow (**1936**) collected *Polyphagus* in Denmark and Britain. He found, in the Danish material, that only the spiny type of

zygospore was present; in the British collection both were present, but the smooth form was predominant. He also examined de Bary's slides from the British Museum (N.H.), labelled "Mai, 1876, glyc. Nowakowski." These specimens, which Sparrow points out can certainly be considered a co-type of the fungus, bore both the spiny and the smooth types of zygospores. In commenting on these zygospore findings, Sparrow (**1936**, **43**) expressed the belief that future cultural studies will establish the existence of two distinct species parasitizing *Euglena*.

Because of this controversy, cultural methods have been used in a study of this fungus in order to determine whether *P. Euglenae* characterized originally by Nowakowski and later by others constitutes a single species or whether it and *P. Euglenae* var. *minor* represent two distinct species with somewhat similar thalli and dissimilar zygospores. During the spring of 1941 and again in the fall of 1944 collections of *Euglena* were made in farmyard puddles and other likely habitats in order to obtain material for this study. Thalli of the fungus appeared within three or four days in material collected at the following four sites:

A. Farmyard puddle near Holy Hill, Wisconsin, March 8, 1941.
B. Farmyard puddle on Albert Wittl farm, highway U. S. 18, 3 miles east of Jefferson, Wisconsin, April 11, 1941.
C. Pool below artificial waterfall, Lake Park, Milwaukee, Wisconsin, June 4, 1941.
D. Farmyard puddle ½ mile east of Mapleton in northeast corner of Waukesha County, Wisconsin, November 13, 1944.

Cultures from these four collections were designated A, B, C and D respectively and are referred to hereafter under these designations. Liquid cultures were prepared by adding zoospores and thalli to growing cultures of *Euglena viridis;* these were maintained by adding *Euglena* cells from stock cultures at frequent intervals as required and by making transfers to fresh liquid cultures. Other cultures were obtained by growing the host on agar plates of synthetic medium, hereafter referred to as *Euglena* plates, and inoculating with zoospores of the fungus when the surface of the plate was well tinged with green. It was possible, with these two

methods, to keep vigorous stock cultures of A, B, and C until December, 1942 and of D until April, 1945.

In all vegetative stages the thalli in the four culture lines appeared somewhat similar and could not be distinguished from *P. Euglenae* as described and figured by Nowakowski (**1876**, **78**), Dangeard (**1900–01**) and Wager (**1913**). Since the anatomy and development of the vegetative stages are so well known from the excellent works of these early investigators, no detailed account is included here.

As each of the cultures became from three days to two weeks old and zygospores were produced, it was noted that differences existed in those formed in cultures A and C from those in culture B. These differences corresponded with those found between zygospores in single collection cultures by most students of this fungus. The zygospores of series A and C were similar in being smooth-walled while those of series B were spiny-walled and differed from the former in other additional characters as well. Both types of zygospores were found in culture D. In these cultivated specimens it was possible to follow the sequence of events leading to formation of both spiny and smooth zygospores. In no case was the latter formed by enlargement of the extruded contents of a female thallus following its fertilization by a male conjugation tube as described originally by Nowakowski (**1876**). Except for variation in detail, there is but a single conjugation process in which the zygospore is formed at the distal end of a delicate conjugation tube and in contact with or near the larger of the two thalli. The bulk of its body is composed of the protoplasmic contents of the two gametangia which flow to the tip of the conjugation tube where they become confluent and eventually are set off by distal and proximal septa. In formation of the spiny form the protoplasmic mass which represents the incipient zygospore assumes a subapical position in the conjugation tube so that it later is connected with each of the attached thalli by a tube. These observations therefore confirm Nowakowski's later description (**1878**) of smooth and spiny zygospore formation. He also pointed out at this time that the smaller thallus should be considered the female one since the mature zygospore wall is

formed by differentiation of a portion of its membrane—the conjugation tube wall. However, it is to be noted that the major volume of protoplasm in the zygospore is contributed by the larger thallus, that in both forms the mature zygospore either is sessile upon or lies close to the larger thallus and that the latter assumes a passive role while the smaller thallus assumes an active one in accomplishing conjugation. The writer concludes from these facts that, if sexual designations are to be applied, the more voluminous and passive thallus should logically be called a female gametangium or oogonium. This is the treatment in all accounts other than that of Nowakowski. (**1878**), and it is being followed in this report.

Unifungal cultures were obtained by one or more of the following methods for each of the collection series, A, B, and C, and for the smooth (DM) and spiny (DS) forms of collections D. These methods were adapted from those used by Couch (**1939**) for the isolation of other chytridiaceous forms.

(1) Single zygospore culture:

A single isolated zygospore produced and lying on the surface of a *Euglena* plate was removed, along with a cylindrical agar plug, by manipulation of a 2 mm. circular cutting tool. This plug was placed on end on a microscopic slide, and after examination verified the presence of but a single zygospore on its circular upper surface, the plug was placed on its side to permit slicing off the upper ½ mm. as a disk bearing the inoculum. This disk was then transferred to a fresh *Euglena* plate and flooded with sterile charcoal water to induce germination.

(2) Multi-zoospore culture:

A single isolated zoosporangium growing on agar was removed, along with an agar plug, as in the method above and introduced into a hanging drop of charcoal water. After the sporangium matured and liberated zoospores, the latter were drawn up along with the liquid of the drop and distributed over the surface of a plate culture of *Euglena* by means of a finely drawn pipette.

(3) Single thallus culture:

A single isolated immature thallus growing on the surface of a *Euglena* plate was manipulated in the same manner as were the zygospores in method (1) above.

Replicates of these cultures were prepared by transferring inhabited blocks of agar to the surface of fresh *Euglena* plates. These replicates were then treated in such manner that any persistence of distinctive zygospore characters, as found to exist singularly in three of the four original cultures, could by no means be attributed to variations in the physical surroundings or to the nature of the nutritional supply. For the most part, these cultures were kept at room temperature and were subjected to intermittent daylight and darkness by virtue of their position at a south window. Culture series were rotated in horizontal and vertical positions from time to time. The smooth and spiny-walled isolates of collection D, which were studied when cultures A, B, and C no longer were available, were handled in a similar manner. It is assumed that the environmental conditions which prevailed during the period of study were not differentially involved in determining zygospore character. *Euglena viridis,* alone, was supplied as the host species for all cultures, and a single culture medium formula was used for all *Euglena* cultures at a given time.

Cultures A, B, C and D, as collected, were kept under observation for 21, 20, 18 and 5 months respectively while the unifungal isolates on agar of A, B and C were under observation concurrently for 13 months. The unifungal isolates of culture D were similarly kept under observation for 4 months. During these periods the zygospores in series A, C and DM maintained all those characters by which they were originally distinguished from those of series B and later from DS. Throughout the period of cultivation no mature smooth-walled zygospores were found in series B or DS, and likewise no spiny-walled ones were found in series A, C or DM. While it was noted that scarcity of food supply (*i.e.,* paucity of encysted *Euglena* cells) and decrease of water content in the agar caused successive groups of zygospores to be measurably smaller, still they were constant in the character of their type.

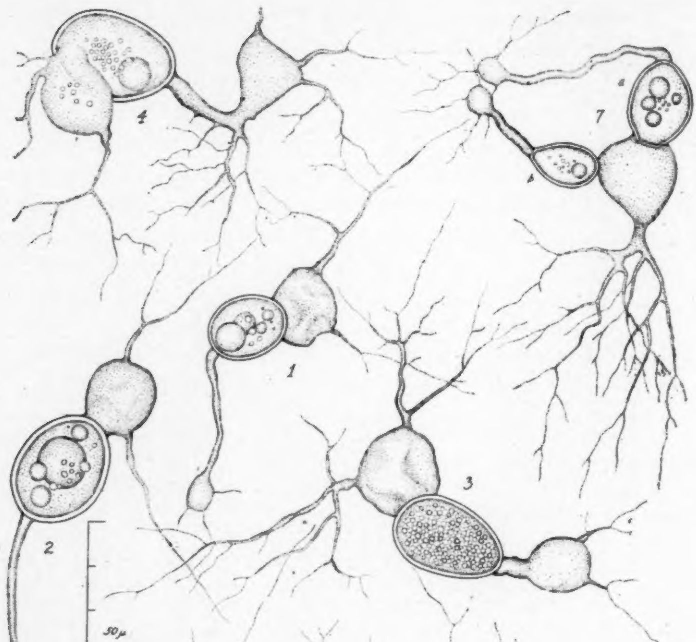
It seems apparent from these data, then, that the nature of the zygospore wall is a persistent and inherited character whose fundamental features are influenced little if at all by environmental conditions. It is concluded that the smooth type is not abnormal and its exospore character is not the result of poor nutritional conditions. In addition to the presence or absence of spines on the surface of the exospore, the zygospores differ from each other in a number of additional features. These differences are shown in table I.

TABLE I

ZYGOSPORE CHARACTER IN CULTURAL ISOLATES

	Isolates: A, C and DM	Isolates: B and DS
Shape	Spheroid, ovoid, elongated, reniform, lacrymoid, clavate, constricted, truncated; considerable irregularity in shape.	Spheroid, ovoid, wide-fusiform; quite regular in shape.
Length	19.6–35.0 μ, av. 26.2 μ	18.0–27.0 μ, av. 22.6 μ
Width	14.0–28.2 μ, av. 19.7 μ	10.6–26.3 μ, av. 17.9 μ
Location	Typically sessile on female thallus; attached to male thallus by a tube.	Typically attached to female thallus by a tube, rarely closer to it than 4.9 μ, as far from it as 13.2 μ, av. 8.9 μ; attached to male thallus by a tube.
Wall	Two-layered; exospore and endospore smooth and hyaline.	Two-layered; exospore always more or less spiny, bright yellow to amber; endospore smooth and hyaline.

As indicated in table I, the two types of zygospores, with their attached antheridial and oogonial cases, can be distinguished with ease by microscopic inspection. It is to be noted that, while the two forms have been referred to as the "spiny" and the "smooth," they are differentiated by the possession and constancy of other additional characters. The smooth form has never been seen to possess a tube connecting it with the empty oogonial case as in the spiny form (FIG. 12, a), although some specimens appear almost to possess one because of the constriction of the attachment region (FIG. 4). Although it is possible that the spiny form may lack this tube under conditions of extreme crowding of the thalli, none has been seen in cultures of this material.



FIGS. 1–8. *Polyphagus laevis.*

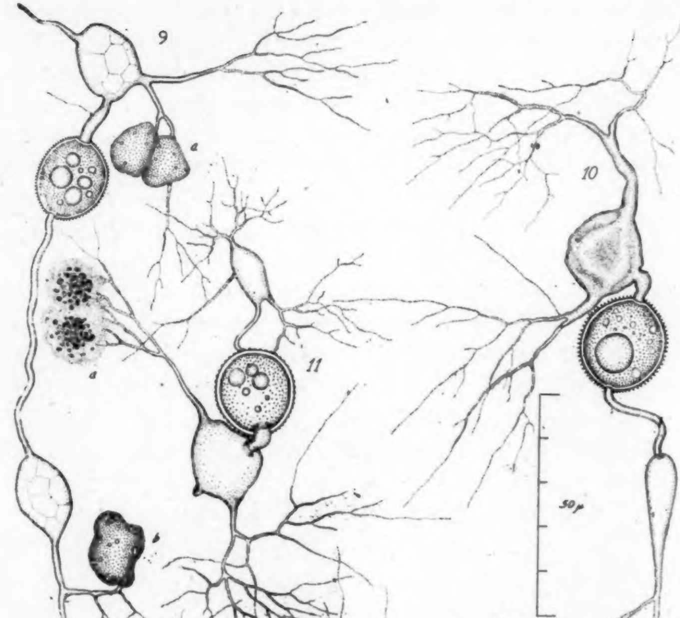
While the thalli illustrated in figures 1 and 2 may be considered typical (*i.e.*, found to be most common in culture), all of the thalli shown in figures 1–8 indicate the basic character of this type. Here, the endospore and exospore are poorly differentiated since both are smooth and hyaline, but at times one may find spores having a faint bluish-green, and more rarely a yellowish tinge. The oleaginous globules, so characteristic as a nutritional reserve, are variable in size and number, but generally there are four or five large globules and a variable number of small ones (FIGS. 1, 2, 6, 7 a). An occasional zygospore becomes completely filled with globules of uniform size, and the cell contents then appear quite dense (FIG. 3). The remainder of the zygospore content is hyaline, homogenous, watery and devoid of granules of appreciable size.

The zygospores shown in figures 1–8 have been selected from cultures A, C and DM as representatives of various developmental types. Figures 1 and 2 show the result of conjugation between a small thallus and a larger one lying at some distance from it. Frequently the zygospore is truncated at its point of contact with the oogonium (FIGS. 7a, 8a). Obviously, in this type, only a small distal portion of the conjugation tube has become intimately involved in the formation of the zygospore, and the remainder has not become inflated. Figures 3 and 5 show the type of development which follows when the antheridium and oogonium lie closer than those referred to above. While a portion of the conjugation tube is still recognizable, the major part of it has become involved in the formation of the zygospore, and the remainder is more or less inflated. The thalli shown in figures 4 and 6 indicate the course of development when the antheridium and oogonium are of similar size. In the first of these (FIG. 4), however, a conjugation tube bearing rhizoids is apparent and indicates the antheridial character of the attached thallus case. When the conjugation tube has become completely inflated in formation of the zygospore (FIG. 6), it is impossible to recognize the sexual nature of thalli such as *a* and *b*. This type of configuration is common and results from the proximity of immature thalli at a time when environmental conditions stimulate sexual reproduction. Thallus *c*, which still possesses protoplasmic contents, apparently has no con-

nection with the conjugating thalli or the zygospore but merely began development in the same locality in the medium.

In addition to the mildly aberrant courses of development described above, a number of abnormal ones have been observed. These have to do with the functioning, in a double capacity, of one or the other of the gametangia. In some instances it appears that an oogonium may be receptive to the tips of the conjugation tubes from two male individuals resulting in the formation of two zygospores attached to the surface of a single female thallus (FIG. 7). Although zygospore *a* is larger than *b*, no fundamental difference between them could be noted by microscopic examination. In other instances evidence was seen to suggest a multiple function by a male thallus (FIG. 8). Although the history of these two zygospores is unknown, the tubular portion between them is interpreted as the visible remains of a male thallus from which a conjugation tube had contacted each female thallus at *a* and *b*. It is curious that oleaginous globules were excluded from the zygospores, one remaining in each of the oogonia. Unfortunately the nuclear history in these two types of abnormality is unknown. From the cytological study of Wager (**1913**) it is known that nuclear divisions occur only in the sporangia; it seems inconceivable, then, that the female thallus of figure 7 and the male thallus of figure 8 should be conveniently provided with a nucleus for each zygospore. It appears more probable that one of the apparent zygospores in each case is a parthenogenetic structure comparable to the cysts produced by the prosporangia but differing fundamentally from the latter in having received nutriment by connection with a female thallus.

In contrast to the smooth form, the exospore of the spiny one varies in color from bright lemon to deep amber and sometimes brown, with some evidence from delicate focusing under high magnification to suggest that the core of the spine is more hyaline than its shell or that the endospore extends into the spine as a hyaline core. The spines, themselves, vary from short, delicate ones which are typical (FIG. 13) to relatively coarse, conical projections (FIG. 10); occasionally the ornamentation may appear as somewhat scattered spines (FIG. 14) and rarely as rounded, short bullations (FIG. 11). Frequently the spines are shorter and more



FIGS. 9–14. *Polyphagus Euglenae.*

delicate at the two ends of the zygospore than over its equatorial region (FIG. 12). The nutritional reserve usually is confined in one or two relatively large globules with a number of additional small ones (FIGS. 10, 12–14). In addition, the cytoplasmic contents appear quite granular and dense although this appearance is enhanced to a considerable degree by diffraction of the light in passing through the upper and lower spine-bearing layers. While usually the constituents of the host cells have been reduced at this stage to an irregular mass of clumped, reddish-colored granules (FIG. 11a), an occasional fungus will be found to attack new *Euglena* cysts late in its course of development so that the host contents are not fully utilized (FIGS. 9a and b).

Some variation in the details of zygospore formation has been noted in this form, but the extremes of variation and the so-called abnormalities, which are common in the smooth form, are strikingly absent. Although the presence of a number of zygospores on the surface of an oogonium has not been seen in this material, it has been noted and figured for the spiny type by Nowakowski (**1878**).

The thallus-zygospore relationship shown in figure 12 has been found to be most common, although the configurations shown in figures 9 and 10 are almost equally prevalent. The predominant type of oogonium is fusiform with a laterally attached communication tube (FIGS. 10–12, 14); other shapes have been seen occasionally (FIGS. 9, 13). The antheridia exhibit considerable variation in shape from fusiform or ovoid with one rhizoidal axis (FIGS. 9, 10, 13, 14) to a more or less irregular shape with several rhizoidal axes (FIGS. 11, 12).

From the foregoing it is apparent that these two fungi can be distinguished with ease during and after the process of conjugation. Upon studying thalli in the vegetative stages, it was found that here, too, they differ sufficiently to permit positive identification. The prosporangia in cultures B and DS are typically fusiform or clavate with an elongated or cylindrical zoosporangium attached in a lateral position (FIGS. 17, 18). Globose prosporangia (FIGS. 15, 16) were fairly common. Frequently the zoospo-

rangium was found to be somewhat elongated with an undulated surface (FIG. 16) and occasionally one was found to be considerably elongated (FIG. 15). The vegetative thalli in cultures A, C and DM characteristically consist of a globose prosporangium and a globose (FIGS. 19, 21, 22), ovoid (FIG. 23) or curved (FIG. 20) zoosporangium. Generally the thalli of this type are smaller and more delicate.

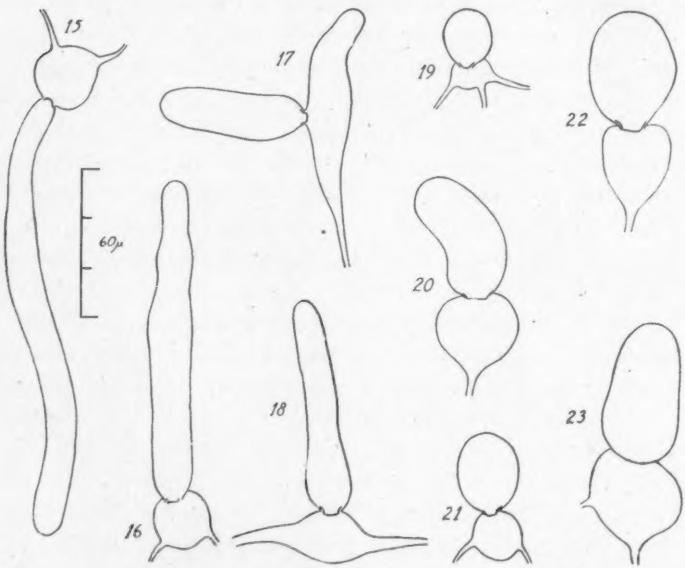
It is concluded from the information obtained in this study that *P. Euglenae,* as the binomial commonly heretofore has been used, represents two genetic entities whose thalli can be distinguished in either the vegetative or the zygospore stage. It is further concluded that the fungus grown in cultures A, C and DM is identical with Nowakowski's *P. Euglenae* var. *minor.* While admittedly our knowledge of genetic relationships as applied to taxonomy in this group of the fungi is extremely meager, it appears that most students prefer to look upon comparable characters in other genera as of specific rank. *Phlyctidium spinulosum* (Sparrow, **1933**), *Phlyctochytrium chaetiferum* (Karling, **1937**), species of *Micromyces, Micromycopsis* and others are differentiated wholly or in part on the possession of thallus, sporangial or resting spore ornamentation. The validity of this practice is unquestioned in most instances, and the use of definite ornamentation as a diagnostic character has almost come to be taken as a matter of course. However, recent cultural studies by Shanor (**1939a**, **39b**) and McLarty (**1939**, **41**) seem to indicate that spines, fibrillae, warts and other types of projections are not, in themselves, diagnostic but may be so when they appear regularly at a given stage in the life history through successive generations.

In consideration of the persistence in culture of the distinctive features of these two fungi, it is the opinion of the writer that *P. Euglenae* var. *minor* is to be considered a species separate and distinct from *P. Euglenae.* It is suggested that the latter name be reserved for those thalli whose zygospores are spiny-walled and which agree in other characters with those tabulated and described for this form; *P. laevis* is proposed as the species name for the smooth-walled form.

POLYPHAGUS EUGLENAE Nowakowski sense nov.

Syn. *P. Euglenae* Nowakowski pr. p. (see Sparrow, **1943**, p. 299).

Prosporangia extramatrical, lying free in the medium, rarely sessile, typically fusiform, clavate, commonly spherical, ellipsoid, elongated or irregular, 7.2–38.4, av. 18.1 μ in diameter × 12.2–200.0 or more, av. 36.2 μ long; with 2–8 rhizoidal axes about 6 μ in diameter at their point of origin, the latter branched and re-branched with their tips imbedded in a number of hosts. Zoospo-



FIGS. 15–18. *Polyphagus Euglenae;* 19–23, *P. Laevis.*

rangia typically lateral on a fusiform prosporangium, usually elongated, tubular and tapering toward the apex, occasionally short-cylindrical or curved, rarely ovoid or ellipsoid, 7.6–36.0, averaging 18.7 μ in diameter × 21.8–179.2 or more, av. 107.7 μ long, with thin smooth wall, opening by an apical deliquescence pore, containing one to many hundreds of zoospores. Zoospores cylindrical to ellipsoid, 3–5 μ in diameter × 6–13 μ long, containing a single posteriorly located pale yellow oil droplet and provided with a long posterior flagellum, escaping individually and generally swimming

away immediately, positively phototactic, occasionally some zoospores germinating inside the sporangium. Antheridia fusiform, clavate, spheroid or irregular, 4.1–14.2, av. 9.4 μ in diameter × 6.6–35.4, av. 16.7 μ long; oogonia fusiform, saccular or irregular, 12.3–21.4, av. 16.3 μ in diameter × 14.8–61.7, av. 26.3 μ long. Zygospore spheroid, ovoid or wide-fusiform, 10.6–26.3, av. 17.9 μ in diameter × 18.0–27.0, av. 22.6 μ long, with a thick, 2-layered wall, the exospore bright yellow to amber or brown and beset with delicate conical spines or rarely with bullations, endospore smooth and hyaline; subterminal on an elongated conjugation tube 6.5–67.2, av. 18 μ long × 1.8 μ in diameter, separated from oogonium by a portion of that tube 4.9–13.2, av. 8.9 μ long × 3.3 μ in diameter; functioning in germination as a prosporangium.

Parasitic on the cysts of various species of *Euglena,* especially *E. viridis* and *E. sanguinia,* and on cysts of *Chlamydomonas Reinhardi* and *C.* sp.; apparently of general occurrence in the northern hemisphere.

Polyphagus laevis (Nowakowski) comb. nov.

Syn. *P. Euglenae* Nowakowski pr. p. (see Sparrow, **1943**, p. 299, 300).

P. Euglenae var. *minor* Nowakowski (see Sparrow, **1943**, p. 300).

Prosporangia extramatrical, lying free in the medium, rarely sessile, typically globose, 12.3–28.4, av. 22.4 μ in diameter, or ovoid, 11.2–26.2, av. 19.2 μ in diameter × 18.4–28.6, av. 24.0 μ long, occasionally irregular in shape, with 1–6 rhizoidal axes about 3 μ in diameter at their point of origin, the latter extensive, branched repeatedly and with their tips imbedded in a number of hosts. Zoosporangium located at any point on surface of prosporangium but typically diametrically opposite the insertion point of the most prominent rhizoidal axis, typically ovoid, 19.2–35.2, av. 27.5 μ in diameter × 25.6–41.6, av. 36.5 μ long, with thin smooth wall, opening by an apical or subapical deliquescence pore, containing several to many zoospores. Zoospores ovoid to elongated, 3.0–3.4, av. 3.3 μ in diameter × 5.0–6.5, av. 6.4 μ long, containing a single posteriorly located, pale bluish-green droplet and provided with a long posterior flagellum, escaping individually and generally swimming away immediately, positively phototactic, rarely germinating inside the sporangium. Antheridia spherical, ovoid or irregular, 4.2–15.4, av. 9.8 μ in diameter × 6.4–23.8, av. 16.5 μ long; oogonia spherical, ovoid or irregular, 14.0–28.2, av. 18.0 μ in diameter ×

15.4–25.2, av. 20.8 μ in diameter. Zygospores ovoid, truncated, spheroid, elongated, reniform, lacrymoid, clavate, constricted, or irregular, 14.0–28.2, av. 19.7 μ in diameter × 19.6–35.0, av. 26.2 μ long, with thick, 2-layered wall, the exospore smooth, hyaline, rarely pale yellow, the endospore smooth and hyaline, terminal on a more or less elongated conjugation tube, 2.8–77.0, av. 28.2 μ long × 1.4–5.2, av. 3.0 μ in diameter and sessile on the larger gametic thallus, functioning in germination as a prosporangium.

Parasitic on the cysts of *Euglena viridis, E.* sp. and on the cysts of *Chlamydomonas* sp.; apparently of general occurrence in the northern hemisphere.

SUMMARY

This study is concerned with clarification of a controversy concerning the relationship and taxonomy of smooth zygospore and spiny zygospore-producing races of *Polyphagus Euglenae* which occur primarily as parasites on various species of *Euglena.*

Thalli from four collections were cultivated in liquid and on agar by supplying them with living *Euglena* cysts. Zygospores formed in cultures from two collections were smooth-walled and sessile on the oogonium while zygospores from one collection were spiny-walled and attached to the oogonium by a tube. Zygospores of both kinds were formed by thalli cultivated from a fourth collection. Unifungal cultures were prepared for the mono-zygosporic collections, and the two zygosporic races of the remaining collection were isolated in unifungal cultures.

The zygosporic character of each isolate remained constant during subsequent cultivation.

The spiny form is identical in part with *P. Euglenae* as originally described; a revised diagnosis is given for it. The smooth form is identical with *P. Euglenae* var. *minor;* it is rediagnosed and raised to specific rank as *P. laevis.*

The process of conjugation is fundamentally similar in both species; this is in confirmation of Nowakowski's observations.

ACKNOWLEDGMENTS

The writer is indebted to Professor E. M. Gilbert of the University of Wisconsin for helpful criticisms in preparation of the

manuscript and to Mr. Szymon St. Deptula, also of the University of Wisconsin, who gave willingly and freely of his time in translating Nowakowski's Polish paper. It is a distinct pleasure to express appreciation of these valuable aids.

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EXPLANATION OF FIGURES

All figures were drawn from living material with the aid of an Abbe camera lucida, using a 10 × ocular and a 4 mm. objective; original magnification of figures 1–14 is 1500 × following enlargement by means of a pantograph, and original magnification of figures 15–23 is 750 ×.

FIGS. 1–8. *Polyphagus laevis*. 1–2, typical proportional relationship of zygospore to antheridium and oogonium; 3, zygospore with atypically dense contents; 4, zygospore with gametangia of approximately equal size, the antheridium provided with a tube; 5, zygospore with antheridium attached by an abnormally short tube; 6, zygospore with attached sessile gametangia, a and b, whose sexual nature is not apparent; c, immature thallus merely growing in the vicinity; 7, oogonium to which two zygospores and their connected antheridia are attached; 8, antheridium that has conjugated with two oogonia resulting in the formation of a zygospore at a and at b.

FIGS. 9–14. *P. Euglenae*. 9, typical zygospore connected to fusiform antheridium by an elongated tube; parasitized *Euglena* cells at a and b; 10, zygospore connected laterally to fusiform oogonium and apically to a clavate antheridium; 11, zygospore beset with delicate scattered bullations; mass of granules at a represents the remains of two *Euglena* cysts; 12, appearance of typical zygospore, oogonium and antheridium, the former with more delicate spines at the two ends; 13, zygospore with uniformly distributed spines of equal size; 14, zygospore with widely scattered spines of uniform size.

FIGS. 15–18. *P. Euglenae*, sporangia and prosporangia.

FIGS. 19–23. *P. laevis*, sporangia and prosporangia.

SPECIES OF SYNCHYTRIUM IN LOUISIANA
II. SPECIES OF LOUISIANA SYNCHYTRIUM

Melville T. Cook

(with 1 figure)

This is a record of five species of *Synchytrium* found in the vicinity of Baton Rouge, Louisiana, between January 4 and April 12, 1945. Three of them appear to have been previously undescribed. The descriptions in this paper are based on fresh material.

Synchytrium Erigerontis sp. nov.

This species attacks the epidermal cells in basal leaves of *Erigeron philadelphicus* L. causing them to turn yellow. The galls start as very small green papillae visible on either surface but rarely visible on both. A few were found on the stems. They are more abundant on the margins than on other parts of the leaves, and turn black with age. There is no evidence of a gall until the fungus is about half its full size. The fungus may be entirely submerged in the tissues of the host plant except for the opening to the surface, but in most cases one-half is submerged in the tissue of the leaf and the other half in the gall, which projects above the surface. No true galls are formed in the former type of infection, but the enlarged infected cells frequently extend from epidermis to epidermis. The opening leading to the infected cell is always visible if the sections are cut properly. The leaf may be slightly thickened or about twice as thick as normal. The host cells around the infected cells are not modified but are replaced by the enlarged, infected cells. When the infected cell is ready for segmentation it measures 126–167 μ. The fungus is yellow, becoming orange-colored, 45–160 μ in diameter; when mature it is surrounded by a thick, yellow wall consisting of three layers. The

inner layer is almost hyaline. The middle layer is thick and so brittle as to break readily, but becomes thin at maturity. The disintegrating contents of the host cell is yellow or black and 5–15 μ in thickness but the host nucleus is rarely seen. When two sori occupy the same cell they are hemispherical in form.

Gallis parvis, colore a viridi usque ad nigrum differentibus in utraque superficie marginum foliorum basalium depressis aut semi-depressis in folium, 126–167 μ in diametro. Soris colore a flavo usque ad aurantium differentibus, 45–160 μ in diametro.

Hab. *Erigeron philadelphicus* L.

Synchytrium Stachydis sp. nov.

This species attacks the epidermal cells and causes galls of various sizes, usually on the upper surfaces of the leaves and on the petioles and stems, and occasionally on the lower surfaces of the leaves of *Stachys agraria* Cham. & Schlecht. The epidermal cells surrounding the infected cells grow and cause galls composed of two or more layers of large, thin-walled cells. In many cases the epidermal cells of the galls become infected and large compound galls are formed. The thickening of the leaves causes the galls to be about one-half submerged. The galls are large, compound, and usually the result of infection of the epidermal cells of the galls by the fungus. They are variable in form; the single galls are almost spherical and on short pedestals which are cylindrical or almost columnar but slightly constricted at the base. This character is usually lost in compound galls. The galls are green, sometimes light green, becoming brown. The galls may start to form very soon after infection of the epidermal cells or may be delayed until the fungus is about one-half full size. The infected cell is surrounded by the growth of the host tissues until about half grown; at that time the gall begins to form. There is little or no distortion of host tissues within the leaf. The galls are usually crowded into a mass and cause thickenings of the leaves. The infected cells are never completely covered by the growth of the surrounding cells, but some have a much larger aperture than others. The aperture always enlarges with maturity. Simple galls measure 100–200 μ, compound galls 220 μ or more. They are composed of parenchyma cells.

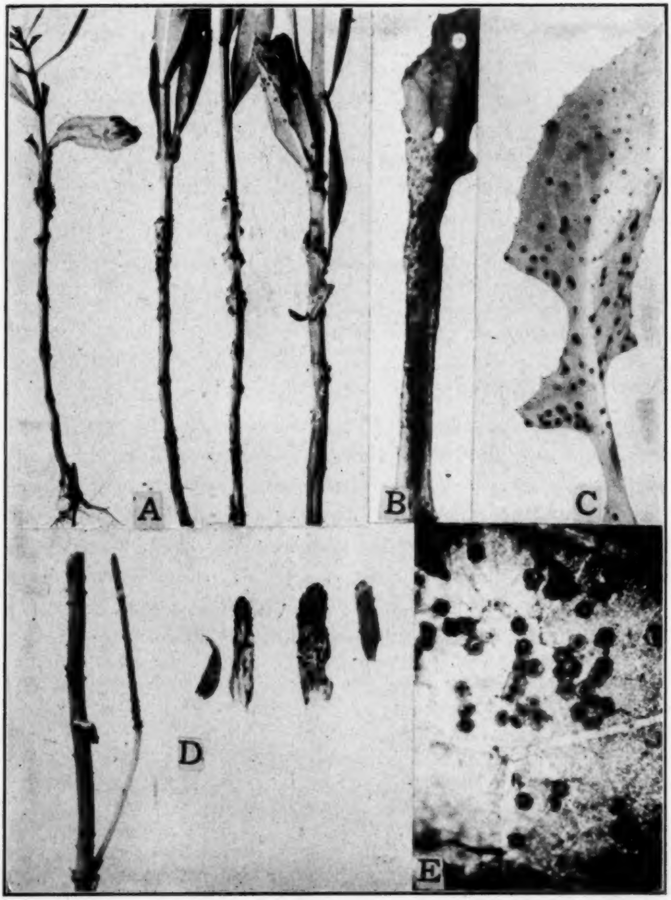

FIG. 1. A, *Synchytrium Lythri;* B, *S. Erigerontis;* C, *S. aureum;* D, *S. globosum;* E, *S. Stachydis.*

The fungus is yellow, measuring about 60–70 μ, but does not completely fill the infected cell and only a small amount of the host cell material persists. The wall around the fungus forms early, consists of two layers, is thick and hard (but the space between the fungus and the wall of the host cell is usually clear). Two or three fungi may be found in the same cell but are not necessarily the same age, judging by development. The development and formation of sporangia is in the usual manner. Young and old galls may be very close together in a leaf, indicating that the fungus may infect cells of various ages.

Gallis simplicibus et globosis aut compositis, viridibus maximam partem in superficiebus superioribus foliorum, petiolorum et stirpium. Galli simplices nonnonquam in stylobatibus siti, 100–200 μ, soris flavis 60–70 μ.

Hab. *Stachys agraria* Cham. & Schlecht.

Synchytrium Lythri sp. nov.

Hemispherical or oblong galls, numerous, sometimes compound, variable in size, mostly on basal parts of stems, and on leaves and petioles of *Lythrum alatum* Pursh. and measure about 80–100 μ. Leaves frequently thickened. The infected cell is spherical with long neck. The infections are always epidermal but in advanced stages frequently have the appearance of being sub-epidermal. Fungus is yellow and measures about 30–40 μ at maturity. The wall around the fungus is composed of three layers.

Gallis oblongis aut semiglobosis plerumque simplicibus in stirpibus, foliis petiolisque sitis, colore a viridi usque ad subrufum differentibus, 80–100 μ, soris flavis, 30–40 μ.

Hab. *Lythyrum alatum* Pursh.

SYNCHYTRIUM AUREUM Schroeter on *Lactuca* sp.

This species causes leaf galls which are usually concave on the lower side of the leaf and convex on the upper side but sometimes the reverse. Most infections are in epidermal cells on the lower surface but the galls are usually formed on lower, regardless of point of infection. This is different from the galls caused by most species of *Synchytrium,* which cause galls on the same surface as the infected cells. Galls usually start soon after infection but there are variations as to time. A small papilla develops in the center

of the concave side, which is usually on the lower surface. The leaves may be slightly thickened at point of infection without gall formation. The galls are small and green at first but become large with age and the papillae becomes black and about 60–90 μ when mature. The fungus is yellow and 20–30 μ when mature.

This species has been reported from several countries and on nearly 200 species of host plants. In all probability many of these records are incorrect.

SYNCHYTRIUM GLOBOSUM Schroeter.

This species causes small, green pustules on either side of leaves and on stems of *Veronica perigrina* L. They become brown and finally black and measure about 60–80 μ. The infected cells become pear shaped and the basal halves of those on the leaves are submerged in the host tissues while only a very small part of those on the stems are submerged in the cortex. The galls are more or less conical and composed of very large parenchyma cells. The infected cells on the upper surface are usually about half embedded in palisade tissue while those on the lower surface are usually completely embedded in the mesophyll. The fungus is yellow and about 35–40 μ in diameter.

This species is found in northern European countries and in Iceland. It was described in 1870 and has been reported as attacking about twenty species of host plants. The species in Louisiana occurs on an entirely different species of *Veronica* from any previously reported, is only about half the size of the European species and differs in some other details.

The author wishes to express his thanks to the workers mentioned in the first paper and to Dr. Illo Hein for material and other assistance in the work.

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EXPLANATION OF FIGURES

FIG. 1. A. *Synchytrium Lythri,* natural size. B. *Synchytrium Erigerontis,* natural size. C. *Synchytrium aureum,* natural size. D. *Synchytrium globosum,* natural size. E. *Synchytrium Stachydis,* enlarged.

PERICONIA BLIGHT OF HEVEA

John A. Stevenson and Ernest P. Imle

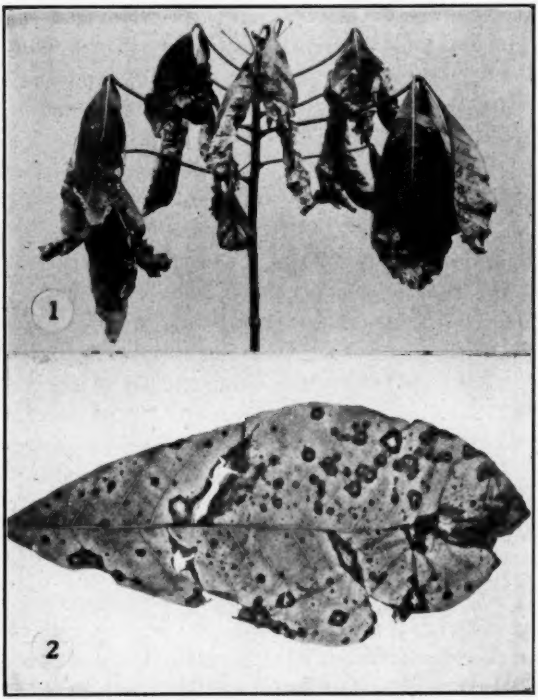
(with 4 figures)

In December, 1943, an unknown disease characterized by a severe leaf spotting was found in a nursery of *Hevea Spruceana* at Turrialba, Costa Rica. Six weeks later, following a prolonged rainy period, this disease had reached epiphytotic proportions in the spruceana nursery where it was causing leaf, petiole, and twig blight, and also was producing minor damage in a nearby nursery of *Hevea brasiliensis* seedlings. In addition to Turrialba (elevation 2000 ft.) the disease was noted near Gualipes, Costa Rica (elevation 600 ft.). An earlier observation of the same disease was made by W. J. Martin on *H. brasiliensis* at El Palmar, Tezonapa, Mexico, but no collections were made.

The leaf spots are circular to oval, at times somewhat irregular or elongated along the veins, but not vein limited, appearing much the same on both surfaces. Primary lesions vary in diameter from two to ten millimeters, but frequently coalesce, particularly on younger leaves, to involve an entire leaf and may bring about premature abscission. The spots are brown at first, becoming ashen at the center with a brown border, and on mature leaves (fig. 1) they are often ringed by a chlorotic halo. Necrotic areas split irregularly and may even fall away in part. Petiole lesions are common and, when severe, cause leaf abrasions or petiole breakage. Petiole lesions or leaf spots sometimes spread down to the leaf axils and cause sunken twig cankers or die-back of young soft twigs (fig. 2).

This disease has been found on *Hevea brasiliensis, H. Spruceana, H. guianensis, H. Benthamiana,* and on hybrids of *H. brasiliensis* × *Spruceana. H. Spruceana* clones selected for resistance to South American leaf blight (*Dothidella Ulei* P. Henn.) are readily attacked. *H. brasiliensis* clones, highly resistant to *D. Ulei,* have been heavily infected when growing under a thin overstory of

heavily infected *H. Spruceana* plants, but these same clones showed almost no damage when grown 20 to 30 feet away from the heavy source of inoculum and out in full light. The following *Dothidella*-resistant *brasiliensis* clones have been damaged, some



FIGS. 1, 2. *Periconia*, blight of *Hevea*.

severely, under the above described conditions: F–409, F–211, F–1620, FB–45, FB–54, FB–79, FB–3363, and FB–3384. F–409 was least damaged.

The disease is very destructive on *H. Spruceana* during prolonged periods of rainy weather, but all evidence at hand indicates that it will not become a problem on the important rubber-producing species of commerce, *H. brasiliensis*, except where this species is grown in a mixture with the highly susceptible *H. Spruceana*.

This combination of species will be used in Latin America only in a few isolated gardens for production of hybrid seed, and artificial means of control could be used in such small areas should the disease become threatening.

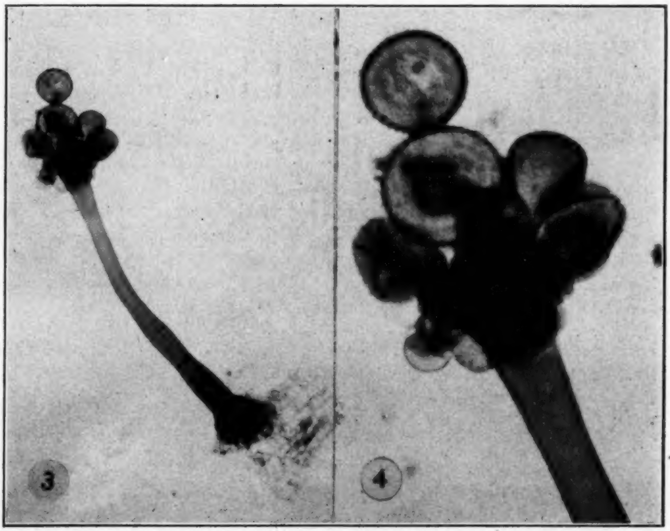
Numerous lesions were produced on leaves and petioles of *H. Spruceana* seedlings without wounding when infected leaves which were sporulating were suspended above young flushes during rainy weather. Infection was also obtained when conidia from diseased leaves were atomized onto wounded and non-wounded three-quarter grown leaves of clone F–6398 (a hybrid of *H. brasiliensis* and *H. Spruceana*). Visible lesions were noted 7 days after inoculation and conidia were produced within 10 days. The pathogen grows and sporulates readily on potato dextrose agar.

The relatively small number of conidia produced per lesion and their large size as described hereafter probably account to an appreciable extent for the slow spread of the disease. Susceptible plants growing beneath a heavy source of inoculum have become seriously diseased in two weeks, while similar plants 300 yards away remained disease free for 3 months or until inoculum was introduced artificially. The disease, though very destructive during prolonged periods of rainy, cloudy weather, is reduced almost to the point of disappearance during the dry season. Viable conidia have been obtained from leaf spots on old leaves infected 5 months earlier, indicating that the pathogen may survive a considerable period of unfavorable weather and initiate new infections when the rains begin again.

A species of *Periconia* has been found constantly associated with diseased areas, which is characterized by relatively large black erect conidiophores bearing terminal clusters of globose conidia (FIGS. 3 and 4). The conidiophores are scattered individually over the lesions and appear on both leaf surfaces. They are readily found with a hand lens and can even be noted without the assistance of this instrument when an infected leaf is held against the light. A *Phyllosticta* is sparingly present on some infected leaves, but appears to be entirely secondary.

Previous reports of the occurrence of *Periconia* on *Hevea* are few. Petch (The Physiology and Diseases of *Hevea brasiliensis*, p. 262. 1911) notes the occurrence of *P. pycnospora* Fres. as a

saprophyte on diseased leaves in Ceylon. This species has conidia only 12–17 μ in diameter and in this and other morphological characters differs markedly from the Costa Rican fungus under discussion. *P. pycnospora* is generally distributed as a saprophyte on stems, leaves, and other plant parts of a very wide range of phanerogamic substrata and cannot be confused with our species.



FIGS. 3, 4. *Periconia*, blight of *Hevea*.

Weir (A pathological survey of the Para rubber tree in the Amazon Valley. U. S. D. A. Bull. 1380, p. 88. 1926) reports the presence of *Periconia byssoides* Pers. on leaves of *H. brasiliensis* associated with *Gloeosporium* and other leaf fungi in the Amazon region of Brazil. Specimens to check this report have not been found. *P. byssoides* is a rather vague species which Saccardo says is not sufficiently distinct from *P. pycnospora*. The name has been used by many workers for a fungus of similar habits to *P. pycnospora*, with which as already indicated it is probably synonymous.

Very few species of *Periconia* have been reported as plant parasites and of these none have been heretofore known on members

of the Euphorbiaceae. The several species described as parasitic on leaves or other plant parts all differ from the *Hevea* species in having much smaller conidia and in other specific morphological characters. Similarly the more numerous saprophytic species all differ along the same lines. The species on *Hevea* is therefore described as new.

Periconia Heveae sp. nov.

Spots amphigenous, circular to irregular, 2–12 mm. in diameter, brown at first, then with ashen gray centers, and deep-brown, definite borders, 1–3 mm. across, not raised; *vegetative mycelium* scanty, intramatrical, light-brown, septate, branching, 3–4 μ in diameter; *conidiophores* numerous, amphigenous, scattered, erect, rigid, unbranched, dark-brown microscopically, black shining macroscopically, without stromatic base, 2- rarely 3-septate, 250–400 μ long (average about 300 μ), with bulbous basal cell 45–90 μ long, 24–30 μ in diameter at base, 15–18 μ in diameter above; *apical cell* short clavate, slightly constricted at septum, light-brown, 30–45 × 20–25 μ; *sporogenous cells* in a whorl at base of apical cell, minutely verruculose, 10–15 × 18–24 μ; *conidia* globose, deep brown, strongly verrucose, 25–45 μ in diameter (usually 30–35 μ), short catenulate, terminal conidium only reaching extreme size.

On living leaflets, petioles, and smaller twigs of *Hevea Spruceana* (Benth.) Muell. Arg. (Euphorbiaceae), Turrialba, Costa Rica, Ernest P. Imle, Feb. 5, 1945 (Type, Mycological Collections, Bureau of Plant Industry, Beltsville, Md. 71424); *Hevea brasiliensis* (H.B.K.) Muell. Arg., Turrialba, Costa Rica, Ernest P. Imle, Feb. 5, 1945, Myc. Coll. 71425. Portions of the type collection have been deposited in the herbaria of the Dept. of Plant Pathology of Cornell Univ., the Farlow Herbarium, the New York Botanical Garden, the University of Michigan, and the Imperial Mycological Institute, Kew.

Maculis amphigenis, orbiculatis vel irregularibus, definitis, cinereis, marginibus atro-brunneis, 2–12 mm. diam.; *conidiophoris* amphigenis, rigidulis, multis, erectis, disseminatis, usque 400 μ longis, 15–18 μ diam., 1–2 septatis, nigris, sub microscopio atro-brunneis, ad basin abrupte bulbosis inflatis; *cella terminali* clavata, ad septum leniter constricta, sub brunnea, 30–45 × 20–25 μ; *cellulis sporogenis* verticillatim ad basin cellae terminalis dispositis, concoloribus ellipticis vel ovalibus, verruculosis, 30–45 × 20–25 μ; *conidiis* globosis, dense verrucosis, brunneis, breve et fugaciter catenulatis, 25–45 μ diam.

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EXPLANATION OF FIGURES

FIGS. 1–2. *Periconia Heveae* on *Hevea Spruceana*. Fig. 1, terminal twig showing blighting effect previous to premature abscission; Fig. 2, an infected leaflet.

FIGS. 3–4. *Periconia Heveae*. Fig. 3, conidiophore × 150; Fig. 4, terminal portion of conidiophore × 430. The apparent terminal conidium has floated in and lodged against the larger and true terminal conidium.

CONIDIUM FORMATION IN SPECIES OF ASPERGILLI

GLADYS E. BAKER

(WITH 64 FIGURES)

Relatively little attention has been devoted within recent years to details attending the development of condiophores and conidia in the *Aspergilli.* The genus early drew attention but the first publications need both confirming and amplifying. De Bary's papers on *Aspergillus glaucus* and *Eurotium* (**1854**; **1870**) included no cytological details; Dangeard (**1907**) figured nuclei in cells of some species, but his observations were far from complete for any species. More thorough cytological observations were made by Fraser and Chambers (**1907**) and Dale (**1909**). The most detailed report of nuclei is Wakyama's investigation (**1931**) of chromosome numbers in several species of *Aspergilli.*

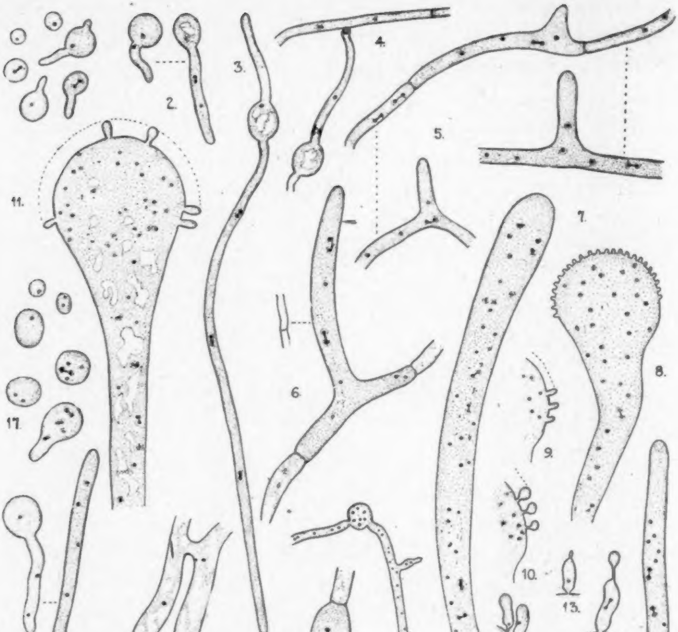
Because of interest in the problem of heterokaryosis and variation in imperfect fungi it seemed important to investigate not only the nuclear condition of *Aspergillus* conidia but also their subsequent stages of development. Even though there is little critical reference material on the subject, the publications describe two types of behavior in conidial development. Dangeard, for example, clearly states (l.c.) for two species, *A. flavus* and *A. fumigatus,* that the conidia are uninucleate. Moreover, he segregated *A. glaucus* as *Eurotium herbariorum,* giving it generic distinction because the conidia were multinucleate. Fraser and Chambers (l.c.) and Dale (l.c.) reported that the species which they investigated, *A. herbariorum* and *A. repens,* had multinucleate conidia at maturity. Thom and Church (**1926**) discuss the occurrence of uninucleate conidia in several other species of *Aspergillus* observed by themselves or others. In addition they refer to Dangeard's multinucleate series (the *A. glaucus* group) and suggest that if this condition obtains for the entire *glaucus* group that it

then forms a distinct line in the entire series of *Aspergilli*. But these observations are not supported beyond their statement.

In this investigation four species of *Aspergilli* have been employed: *A. echinulatus* (Delacr.) Thom & Church (N. R. R. L. strain no. 131); *A. repens* (Cda.) De Bary (N. R. R. L. strain no. 17), both of the *A. glaucus* series as defined by Thom and Raper (**1941**); and two antibiotic producing species, *A. clavatus* Desm. and *A. fumigatus* Fres., both from the laboratories of Dr. S. A. Waksman. The methods of study were the same as those used in an investigation of *Penicillium notatum* (Baker, **1944**), supplemented by sections cut in paraffin at 3, 5, and 7 μ. By the latter method mature conidiophore stages which are mostly too large for the agar-film method could be handled to better advantage. All slides were stained by Heidenhain's iron-alum haematoxylin schedule.

Morphologically *A. clavatus* and *A. fumigatus* differ in conidiophore origin as the former possesses a foot-cell which the latter lacks. Cytologically there is little difference in the details of their conidial formation. In fact their nuclear cycles offer no critical differences as far as possible nuclear distribution and heterokaryosis are concerned.

When first formed a conidium of *A. fumigatus* is uninucleate. At germination the conidia may still be uninucleate or they may have become binucleate through a single mitotic division. Uninucleate, ungerminated conidia usually are much smaller in diameter than the germinating conidia, hence are readily distinguished. At germination a single germ tube emerges though occasionally a second one is formed almost as soon as the first one (FIG. 1). By the time the germ tube is of a conspicuous length the cell is binucleate usually. One nucleus migrates into the elongating tube, there to divide further, and the other remains in the body of the conidium proper (FIG. 2), moving out into the second germ tube later. Usually the formation of the second germ tube is delayed until two or more nuclear divisions have taken place in the first germ tube (FIG. 3). The nucleus which was left in the conidium does not divide until it moves into the second germ tube. Often the second of the germ tubes is shorter and it soon anastomoses with the longer, first formed hyphal out-



FIGS. 1–23.

growths of other conidia (FIG. 4). Anastomoses are frequent at the 25 hour growth level, but are neither so abundant nor striking as those seen in *Penicillium notatum*. The mycelium in its early stages is non-septate. Much later septa may appear forming cells with one or more nuclei. In active stages of growth the nuclei divide freely in the mycelium (FIG. 5).

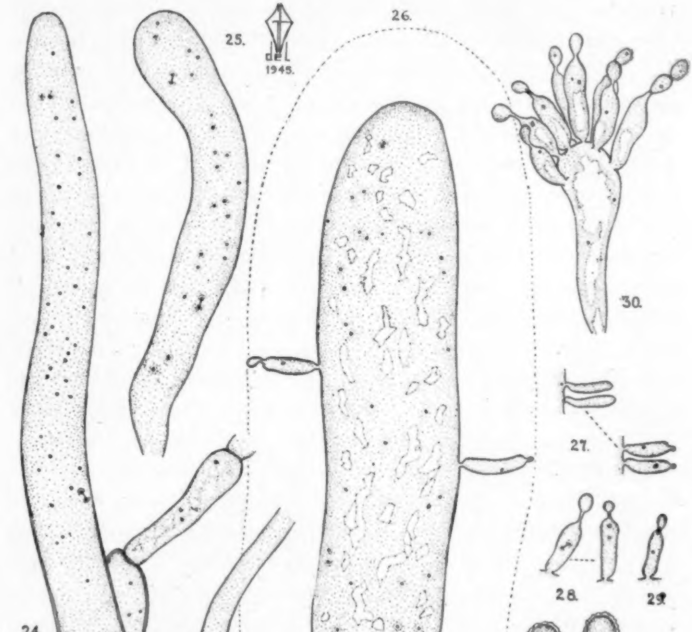
Slide cultures about 40 hours old show a good distribution of conidiophores in varying stages of development. A pair of septa in a hyphal strand ultimately delimits the plurinucleate initial cell of the conidiophore. As the mycelial strand from which a conidiophore arises is multinucleate following anastomoses, the nuclear distribution in the region of the conidiophore initial is not necessarily identical. The initial cell puts out a branch at right angles to the main hypha which enlarges into the conidiophore. It appears that this branch receives one nucleus followed by several others; the nuclei sometimes are already in division as they move into the elongating conidiophore. However, since no septum separates the two parts of the conidiophore there seems to be no way of knowing whether the several nuclei in a young conidiophore originated from one or more nuclei. The nuclei divide actively as the conidiophore elongates and increases its diameter in the distal portion. Incipient phases of the conidiophores are easily recognized because the cytoplasm is densely aggregated even before the septa form; in addition the diameter of both the initial cell and the budding portion is considerably in excess of the diameters of the adjacent assimilative hyphae (FIGS. 5, 6). Conidiophores may also arise directly from a conidium or from the products of several fused conidia.

Developing conidiophores are densely filled with cytoplasm accompanied by many actively dividing nuclei. At maturity the apex expands into the large flask-shaped vesicle, also multinucleate, and the stalk and basal portions become more or less vacuolated. A few scattered nuclei remain in the stalk (FIG. 7). Phialides develop simultaneously as budding protuberances over the entire upper vesicle surface (FIGS. 8–11). Each phialide is in open communication basally with the vesicle at all times. One nucleus moves into each phialide when it is nearing its full size (FIG. 12). When a phialide is mature a fine projection appears

apically which enlarges into the first conidium. Conidium and phialide remain in connection by means of a narrow canal-like tube. The nucleus of the phialide divides once while the conidium is forming and one of the daughter nuclei moves through the canal into the spore, attenuating as it passes through the narrow connective (FIGS. 13–16). All the nuclei of the conidiophore do not enter conidia; some remain in the vesicle and the stalk, the latter by this time is usually quite vacuolate. Successive conidia appear to be formed acropetally in similar fashion.

For *Aspergillus clavatus* the process of phialide and conidium formation on the vesicle is identical with that of *A. fumigatus*. Every phialide has a single nucleus and it produces a series of uninucleate conidia. Successive stages of development of these two species differ in the details of the stages between conidial generations, although essentially the processes involved are the same in that they both allow for the possibility of free nuclear interchange before the next generation of conidiophores produces conidia.

When a group of conidia is inoculated onto the surface of an agar film on a slide, the nucleus of the conidium undergoes several divisions within the first 12 hours, so that the spore may contain anywhere from two to six nuclei before the emergence of a germ tube can be detected (FIG. 17). Typically one nucleus remains in the body of the spore, and the rest continue to move out into the elongating hyphae and divide there (FIG. 18). Anastomoses are common after 21 hours. By then a second germ tube has appeared and soon enters into anastomosis with another hyphal strand (FIG. 19). The original conidia are often still strikingly multinucleate at this stage. As the hyphae grow in a radial pattern from the focus of the inoculum, the aseptate mycelium branches freely and it contains many nuclei well distributed throughout the strands, with the exception of the growing apices themselves (FIG. 20). Later, after 40 hours growth, more fusions occur between hyphae. As portions of the mycelium become septate and much enlarged they form the initials of the foot-cells preliminary to conidiophore production (FIGS. 21–24). The interrelations of these fusing cells is often complex and can be followed best on agar-film slides, since they usually do not lie in a common plane. Foot-cell initials stand out clearly in such preparations by



FIGS. 24–36.

virtue of their denser cytoplasm and heavy walls. These initials have more than one nucleus and by mitotic divisions soon increase the original number markedly. Foot-cells may occur in clusters following anastomosis, but a single group of cells segmented from the hyphal strand gives rise to one conidiophore by budding and subsequent elongation. From the beginning the conidiophore is multinucleate, the number of nuclei increasing enormously up to the time of vesicle formation (FIGS. 25, 26). As in the preceding species, conidiophores occasionally are direct products of conidial germination, or arise from close interconidial fusions. Each conidiophore expands to a clavate vesicular apex from which the phialides are produced simultaneously. At maturity each phialide then buds out a succession of uninucleate conidia (FIGS. 27–30).

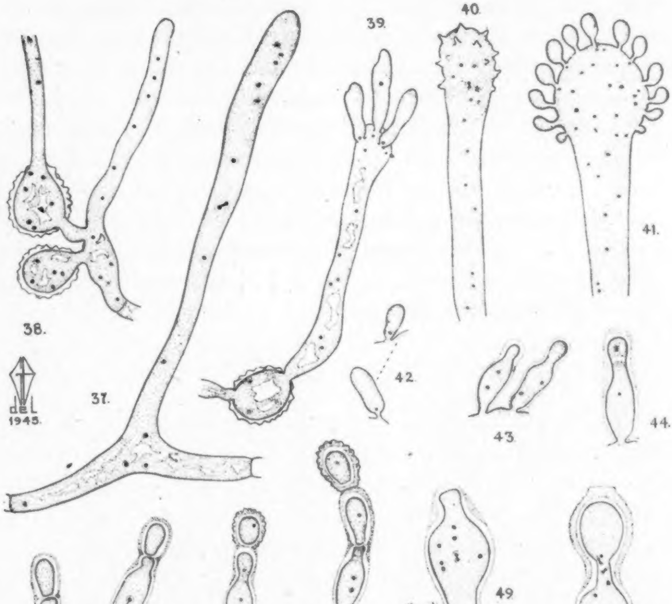
Aspergillus repens and *A. echinulatus* are species without foot-cells belonging to the *A. glaucus* group. The species included in that group have in common, according to Thom and Raper (l.c.), the production of conidial heads borne on septate stalks and perithecia of homothallic origin (the latter character holds for all but one species). Of those producing perithecia further subdivision is made on the basis of ascospore size, large or small. *A. repens* belongs with the small-spored forms. Its conidia vary considerably in size as they increase greatly between the time of their formation and germination. Spores removed from the surface of a culture into a drop of nutrient medium on the surface of a slide spread with Mayer's adhesive and allowed to come just to the drying point before killing and fixing in Bouin's fixative, will show a range from formation size to germination size with their attending nuclear conditions (FIG. 31). Newly formed conidia are uninucleate. Nuclear divisions and increase of spore size are concomitant until at germination the conidia are multinucleate (FIG. 32). Next a single germ tube emerges and into it some of the nuclei move (FIG. 33). Later a second germ tube may appear (FIG. 34). It often fuses with a hypha derived from another spore (FIG. 35). The original spores may contain several nuclei at this and successively later stages. As the hyphae develop the nuclei become dispersed at long intervals and only infrequent septa divide them into multinucleate cells. Conidiophores are produced more or less at right angles as direct outgrowths from a cell of the

mycelium (FIGS. 36, 37), or from the combined products of germ tube anastomoses (FIG. 38), or directly from a single germ tube not concerned with any fusion (FIG. 39). The last condition was one illustrated by De Bary in his 1870 paper. The conidiophore initial is multinucleate and several nuclei move into the developing stalk of the conidiophore where they multiply freely as it elongates and increases in diameter (FIGS. 40, 41). The typical mature conidiophore consists of a terminal dome-shaped vesicle supported on a long stalk which is sometimes septate. It is multinucleate throughout. The stalk becomes vacuolate as the vesicle matures. At that time most of the nuclei are aggregated in the vesicle end. Phialides bud out over the upper surface. As a phialide nears maturity one nucleus moves into it from the vesicle without any alteration in form as the connective between vesicle and phialide is of generous size. The single nucleus of the phialide divides once and one of the two nuclei subsequently passes into the first formed conidium, again without attenuation because of the comparatively large connective between phialide and conidium (FIGS. 42–47). The conidium is separated from the phialide by the deposition of a septum which soon increases into a wide separation band. At the same time a heavy wall is deposited on the outer surfaces. This process gives eventually a series of thick, rough-walled, uninucleate spores (FIG. 48). Several of the nuclei remain in the vesicle and stalk even when many of the spores have been formed, but both structures are by then conspicuously vacuolate. The conidiophores which come directly from spores or unanastomosed hyphae are definitely smaller although their conidia are formed in identical fashion (cf. FIGS. 39 and 41). Such conidiophores resemble the small and short conidiophores found in the *A. glaucus* group on the aerial mycelium. Fundamentally none of these small forms differs from the large type.

The nuclear condition of the conidia in *A. echinulatus* differs greatly from the three species already described. From a comparison of whole mounts (agar-film method) and sections, it is apparent that more than one nucleus moves into the conidium from the phialide on which it is formed. Since the microdimensions of this species are comparatively very large the process of spore formation shows particularly well. The phialides themselves are

multinucleate as nuclei from the vesicle move in abundantly through the ample opening between the two parts, and continue to do so as successive conidia are cut off (FIGS. 49, 50). The first conidium develops as a budding apical protuberance, surrounded by a sheath which is continuous with that over the surface of the vesicle. As the conidium rounds up and its connective with the phialide becomes more pronounced, the sheath becomes noticeably heavier in the connective region and also on the distal surface of the conidium itself. Several nuclei move unchanged through the wide opening (FIGS. 51–53). As many as four nuclei have been seen moving into a spore, and possibly more may enter. Although a cursory glance may suggest that many more than that are moving into the conidium, closer observation shows that several stay in the connective region, the distal portion of which will enlarge to form the next conidium (FIG. 51). Often the nuclei are already in a division stage as they move through the connective region or as they enter the spore, and this adds to the impression of larger numbers of nuclei moving into the spore (FIG. 52) than actually do. Moreover, nuclear divisions in the phialide are infrequently seen. Nuclei continue to move into the phialide from the vesicle as successive conidia of a chain develop. When several conidia have formed in a series it is easy to trace the entire sequence of wall formation. The sheath becomes heavier around the spore but leaves a thinner area between spores so that, upon subsequent separation prior to complete maturity, joined conidia show the sheath becoming echinulate on the free outer surfaces, but still present between them; or if the conidia separate early, the sheath is visible as a little flange (FIGS. 54–56). This is the "disjunctor" region commonly referred to in descriptions of *Aspergillus* spores.

Before a conidium germinates several mitotic divisions have taken place, making it multinucleate unquestionably (FIG. 57). A germinating conidium sends forth a germ tube into which several nuclei move and multiply (FIGS. 58, 59). The number and size of these nuclei are spectacular features of this species. Septa may be laid down in the germ tube near the original spore body, but cross-walls are infrequent typically. A second germ tube from a conidium is not uncommon (FIG. 60). Later (48 hours) some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FIGS. 37–58.

anastomosis among hyphae can be seen. Conidiophores appear at right angles to the assimilative cells, multinucleate from their inception, and enlarge into terminal vesicles which produce a mass of big phialides over their upper surfaces (FIGS. 61–63). The stalks may become one or more septate, a wall often appearing at the base of the vesicle itself. The vesicles have heavy walls with distinct openings into the phialides. The latter show clearly in tangential sections of conidiophores which reveal the openings are from 1–2.5 μ in diameter (FIG. 64). Smaller conidiophores on the aerial mycelium are not unusual. Structurally and cytologically they are identical with the larger ones.

DISCUSSION

This investigation is in agreement with Wakyama's (l.c.) report of uninucleate phialides and conidia in *A. fumigatus* and *A. clavatus,* nor does it disagree with either Dangeard's (l.c.) publication on the former species, or Fraser and Chamber's work (l.c.) on *A. herbariorum* (one of the *A. glaucus* forms). But the results are distinctly at variance with those given by Dale (l.c.) for *A. repens* and by Wakyama for *A. glaucus.* The difficulties attending any investigation in the *A. glaucus* group of *Aspergillus* are complicated by taxonomic confusion. The genus has venerable historic recognition, beginning with Micheli in 1729. He described the readily identifiable "rough-heads" by the name *Aspergillus.* Shortly thereafter *A. glaucus* was described as a species by Link (**1809**). Thom and Church (**1926**) used *A. glaucus* to designate a wide-spread group of species with well marked common characteristics that indicate close relationship. Taxonomists concur that specific differences in the *A. glaucus* group are valid only when based upon ascospore characters. Unfortunately there is now no means of determining the type of *A. glaucus* Link since no ascospore descriptions are extant.

Since no definite organism can be assigned specifically to *A. glaucus,* it is difficult to tell with what members of the *A. glaucus* group Fraser and Chambers (l.c.) and Wakyama (l.c.) were actually working. From the ascospore dimensions given by the former workers, it would seem that the species they had was a

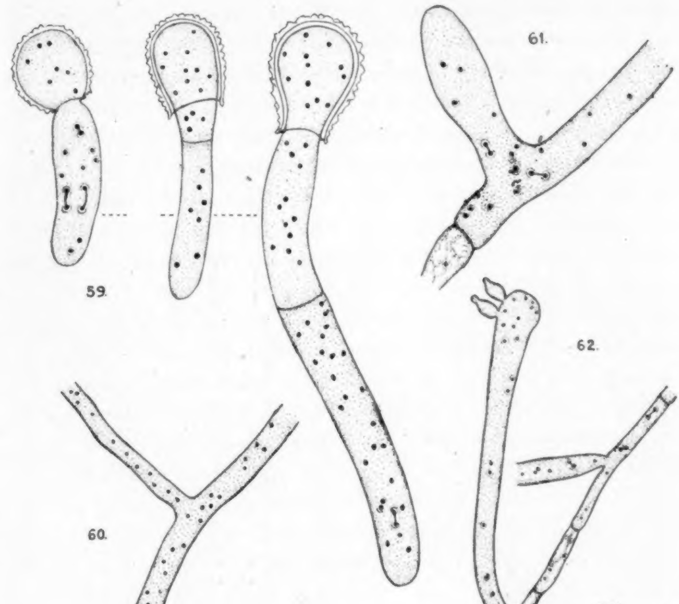
member of the large-spored group, the section in which *A. echinulatus* is classified. Dale's report on *A. repens* emphasizes the similarity of her species and that used by Fraser and Chambers, except for the consistently smaller dimensions of *A. repens*. The identity of *A. repens* does not seem to be in question, so publications relating to that species can be compared directly with this report. But records for *A. echinulatus* can be compared with those on *A. herbariorum* and *A. glaucus* only with the reservation that these forms may not be identical but merely similar.

Dangeard's segregation of *Eurotium* from *Aspergillus* on the basis of nuclear numbers in the conidia is one that has never been widely followed. His cytological figures are not too convincing so it is not surprising that the suggestion had little attention. According to Dangeard the conidia of *E. herbariorum* each contains two to three nuclei. Phialides also were described with four to five nuclei per cell. Fraser and Chambers described the passage of several nuclei to each sterigma (phialide) and several thence to each conidium (*A. glaucus*). At maturity each conidium was said to contain about four nuclei. As seen in *A. echinulatus* each conidium has two or more nuclei entering it but these divide so freely that the mature spore prior to germination may have as many as eight or more nuclei. However, genetically the total number is not so significant as the fact that more than one nucleus is present from the beginning.

According to Dale, *A. repens* has a nuclear history similar to that of *A. glaucus* (*A. echinulatus* of this paper), but her observations could not be confirmed with the *A. repens* examined. There is no doubt that the conidia in the form studied are formed as uninucleate cells but nuclear divisions within the spores make them multinucleate before germination. Not only are the conidia uninucleate at first, but each phialide is also uninucleate and by mitotic divisions provides a nucleus for each successive conidium formed. Dale did not illustrate all stages of conidium production and it is possible that she mistook pre-germination conidia for the formation stage. The cells in this species are small and appearances could easily be misleading. The conidia could be called multinucleate at maturity (before germination) but genetically this is of no importance since all the nuclei are derivatives of one origi-

nal nucleus and therefore are presumably homokaryotic in any one chain of conidia. However, differences could exist between chains as the nuclei entering the conidiophore initial might not be identical. Wakyama (l.c.) reported similar findings for thirteen different species of *Aspergilli* including *A. clavatus, A. fumigatus,* and *A. glaucus.* Again the identity of *A. glaucus* would be open to question. Since both *A. echinulatus* and *A. repens* represent species of the *glaucus* group with demonstrable differences in their nuclear behavior, Wakyama may have been working with a species of the *A. repens* pattern. Whelden (**1940**) likewise found *A. niger* typically had uninucleate phialides and conidia.

It appears that phialides and conidia when first formed in three species of *Aspergilli,* are consistently uninucleate, and that the multinucleate condition in the spores is secondarily derived prior to germination. Consequently if the conidia in these species are homokaryotic in nature it raises the question of the chances of heterokaryosis in such forms. In *Aspergillus fumigatus* by mass spore transfer the mycelial strands as they develop anastomose freely. Eventually multinucleate conidiophores arise from multinucleate segments of the mycelium. Thus if any nuclear variation already exists or is introduced (by mutation) the anastomoses would allow for the redistribution of whatever heterokaryotic types existed. Similarly in *A. clavatus* redistribution can come through anastomoses and the fusions attending the development of the foot-cells. For both of these species the use of monoconidial transfers should perpetuate strictly homokaryotic lines, provided no mutations occur. For *Aspergillus repens,* the third species with uninucleate conidia, single conidial transfers again should reproduce homokaryotic lines, but here the case is complicated because this species represents a homothallic perithecial line, genetically bisexual. The homothallic condition can be shown by single conidium transfers isolated at about the 24 hour stage and transferred to separate petri dishes where they will produce fertile ascocarps and ascospores within two weeks. This is well known for other homothallic perithecial fungi, *e.g., A. Fischeri,* a species similar to *A. fumigatus* (Greene, **1933**); and also many species of *Penicillium* (Emmons and Dodge, **1931**; Dodge, **1933**; Emmons, **1935**). As the usual practice of culture transfer involves the re-



FIGS. 59–64.

moval of many conidia and probably ascospores, the chances of separating out variants are slight by that method. Theoretically karyogamy and meiotic segregation should allow for differences among the nuclei. Presumably then single nucleate conidia should show heterokaryotic differences, for factors not sex-linked.

Finally the fourth species under consideration, *A. echinulatus,* introduces another variable since its conidia are multinucleate from the beginning. It is also a homothallic perithecial form. Single conidium transfers produce ascospores within two weeks, but the growth on the plates is obviously less vigorous than on plates prepared by mass spore transfer. Since the conidia carry several nuclei, theoretically they could be heterokaryotic or homokaryotic depending on the random distribution of the nuclei entering the spores. Therefore one might expect to find differences among cultures derived by single transfer more readily than in the previous instance. Thom and Raper (l.c.) though, have noted that this species is culturally stable as one strain was consistently subculture for 18 years. Probably the transfers involved over the period were by mass spore transfer, which might be the reason for its stability.

Genetically the history of the *Aspergilli* is still an unknown quantity. Greene's work on *A. Fischeri* (**1933**), which is homothallic and bisexual, led him to conclude that the differences he noted in cultures derived by single ascospore or single conidial lines, were due to variations and not mutations. His original variants were obtained from single ascospore lines and this might indicate simply that he had segregation of somatic characters not sex-linked. Unfortunately Greene did not do any cytological work, nor was he consistent in his use of conidia or ascospores as the sources of his lines, and neither did he attempt to recombine strains that showed departure from the original types. Ames (**1934**) has pointed out for *Pleurage anserina* the bisexual nature of the mycelium originating from uninucleate ascospores. Here fertility is controlled by compatibility factors segregating separately. A similar condition might exist in the homothallic *Aspergilli* but there is no experimental evidence on this phase of the problem yet. Until either a thorough cytological investigation is made for one of these homothallic forms, or experimental work on its genetic

behavior is undertaken, it is futile to speculate on the inheritance mechanisms in these fungi. *Aspergillus echinulatus* promises to be a good form for such investigations as the nuclei are of good size and factorial differences may exist in the nuclei entering the conidia. In addition other large spored members of the genus might profitably be investigated to demonstrate the frequency of the *A. echinulatus* type of conidium formation.

SUMMARY

1. In three species of *Aspergillus* (*clavatus, fumigatus,* and *repens*) the conidia are formed as uninucleate cells on uninucleate phialides.

2. The conidium of *A. fumigatus* becomes binucleate by mitotic division preceding germination. This is accompanied by a decided increase in conidium volume. The conidia of the other two species become multinucleate by several mitotic divisions before germination; likewise the spores at germination show great volumetric increase. There is no genetic significance attached to these divisions. In these species the transfer of a single conidium presumably perpetuates a homokaryotic line, but mass spore transfers would allow for the operation of heterokaryosis through anastomoses, dependent upon differences existing in the haploid nuclei. Since *A. repens* is homothallic and perithecial, it might be expected that karyogamy and meiotic segregation would contribute to differences among nuclei, thereby increasing the heterokaryosis.

3. The conidia of *A. echinulatus* are multinucleate when formed, but the original nuclei entering the conidia divide freely so that before germination the cell may have more than eight nuclei. The phialides are also multinucleate. Nuclei continue to pass from vesicle to phialide as conidia are formed. Transfer of a single conidium may mean the carrying of different characters although there is an equal chance that all nuclei which enter the spore are alike.

4. *A. echinulatus* is homothallic and perithecial; consequently the effects of karyogamy and meiotic segregation must be taken into consideration in relation to the nature of the haploid nuclei.

5. In all the species the hyphae become multinucleate when septa

form. Such segments may develop into conidiophore initials either directly or indirectly (foot-cells in *A. clavatus*). There is no way to determine cytologically whether the several nuclei of the conidiophore initial cells are homo- or heterokaryotic. Depending upon this condition, conidia of different chains on the same vesicle may carry like or unlike nuclei.

6. *A. repens* and *A. echinulatus* represent homothallic fungi, as single conidium isolates produce ascospores within two weeks.

7. The nuclear condition of the conidia of these last two species represents a sharp difference in the cytology of two members of the *A. glaucus* group. If they are both good representatives of that group, the suggestion that the group as a whole differs cytologically from other *Aspergilli* is untenable.

The author wishes to express her appreciation to the Department of Biological Sciences at Stanford University for the privileges of its laboratories which greatly facilitated the completion of this investigation.

VASSAR COLLEGE

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EXPLANATION OF FIGURES

All figures drawn with the aid of an Abbé camera lucida. Unless otherwise indicated the magnification is approximately 1850 ×.

Aspergillus fumigatus:

1. Spores, ungerminated and germinating.
2. Spores at 12 hours germination.
3. Spore with two germ tubes and dividing nuclei; 12 hours.
4. Anastomosis between second germ tube of one spore and hypha from another; 25 hours.
5. Stages in development of conidiophore initials; 40 hours.
6. Older conidiophore with portion of nearby assimilative hypha to show difference in diameters; 40 hours.
7. Maturing conidiophore.
8. Expanding vesicle of conidiophore and first appearance of phialides.

9, 10. Stages in phialide development.

11. Mature vesicle with nearly mature phialides on the upper surface, just prior to nuclear migration.

12, 13, 14, 15, 16. A series of phialides showing the entrance of nuclei in the phialide, division, and passage of one nucleus to the conidium.

Aspergillus clavatus:

17. Spores before and after germination; 12 hours.
18. Germination stages at 12 hours.
19. Anastomosis between outgrowths of two conidia with detail of one conidium, × 390 and 900 respectively; 21 hours.
20. Hyphal tip with actively dividing nuclei, × 900; 41 hours.
21. Initial of foot-cell, × 900; 41 hours.
22. Anastomosis of foot-cells, × 900; 41 hours.
23. Young conidiophore, × 900; 41 hours.
24. Older conidiophore with foot-cell, × 900.
25. Expanding vesicle of conidiophore; 59 hours.
26. Apical portion of mature conidiophore, the zone of phialides indicated in outline.
27. Stages in phialide maturation.

28, 29. Division of nucleus in phialide and passage of one nucleus to young conidium.

30. Small conidiophore from aerial hypha.

Aspergillus repens:

31. Spores before and at germination; direct from surface of colony.
32. Germination stages; 23 hours.
33. Later stage in germination; 23 hours.
34. Development of second germ tube; 23 hours.
35. Diagram of anastomosed hyphae from two conidia with young conidiophores, × 435; detail of one cell from hyphal strand at the point indicated, × 900; 31 hours.
36. Stages in development of conidiophore initials; 31 hours.
37. Young conidiophore, the initial completely walled off; 31 hours.
38. Anastomosis between outgrowths of two conidia and developing conidiophore; 23 hours.
39. Small conidiophore from a conidium; 31 hours.

40, 41. Development of vesicle and phialides; 31 hours.

42, 43, 44, 45, 46, 47, 48. A series of phialides showing development and production of conidia; 48 hours.

Aspergillus echinulatus:

49. Phialide with developing conidium.
50. Nuclei moving into conidium; the nuclei in the connective region may be for the next conidium of the series.
51. Nuclei moving into phialide and others moving into conidium.

52, 53. Conidium formation, some nuclei dividing in the young conidia.

54, 55. Maturing conidia in series.

56. Two conidia separated from chain showing disjunctor between them.
57. Mature conidia.
58. Germination of conidium; 22 hours.
59. Germination stages; 22 hours.
60. Hyphal outgrowths from a conidium; 31 hours.
61. Conidiophore at 72 hours.
62. Young conidiophore; 72 hours, × 375.
63. Vesicle with mature phialides and conidia.
64. Phialide openings as seen on surface of vesicle.

STUDIES IN THE GASTEROMYCETES XI. THE GENERA TRICHASTER AND TERROSTELLA

W. H. Long

(WITH 4 FIGURES)

This paper discusses the taxonomic status of three old genera, *Trichaster* Czern., *Geasteropsis* Hollós, and *Geasteroides* Long, reduces *Geasteropsis* to synonymy, renames *Geasteroides*, and redescribes the three species found under these genera.

The *Geasterae* form a well defined group consisting of four genera separated as shown in the following key:

KEY TO GENERA

1. Endoperidium without a sterile base ....(2)
1. Endoperidium with a prominent sterile base ....(1) *Terrostella*
2. Endoperidium persistent, normally with one mouth ....(2) *Geaster*
2. Endoperidium persistent, normally with several mouths ..(3) *Myriostoma*
2. Endoperidium caducous, with a persistent, subligneous columella (4) *Trichaster*

The genera *Geaster* and *Myriostoma* do not need any discussion, but *Trichaster* and *Terrostella* are little known to mycologists. *Trichaster* was discovered and described by Czerniaiev (**1845**) on the Steppes of Russia. Lloyd (**1904**) gives a description and history of this genus, and with his photograph of the type makes it easy to identify. According to Lloyd Czerniaiev sent abundant specimens from the type locality to Berkeley and to Fries.

TRICHASTER Czern. Bull. Soc. Nat. Moscou **18**[2]: 149. 1845.

Geasteropsis Hollós, Novenyt. Kozlem. **2**: 72–75. 1903.

Peridium double; *exoperidium* splitting into stellate, reflexed, coriaceous, persistent segments; *endoperidium* fragile, caducous; *columella* persistent, subligneous, compact.

TYPE SPECIES: *Trichaster melanocephalus* Czern.
DISTRIBUTION: Europe; Africa.

TRICHASTER MELANOCEPHALUS Czern. Bull. Soc. Nat. Moscou **18**[2]: 149. 1845.

Sporophore epigeous, becoming expanded at maturity, 5–8 cm. tall by 3–8 cm. wide; *exoperidium* hard, rigid, coriaceous, splitting beyond the middle into 5–8 unequal rays which bend strongly backward and downward (not fornicate), unsplit area around columella

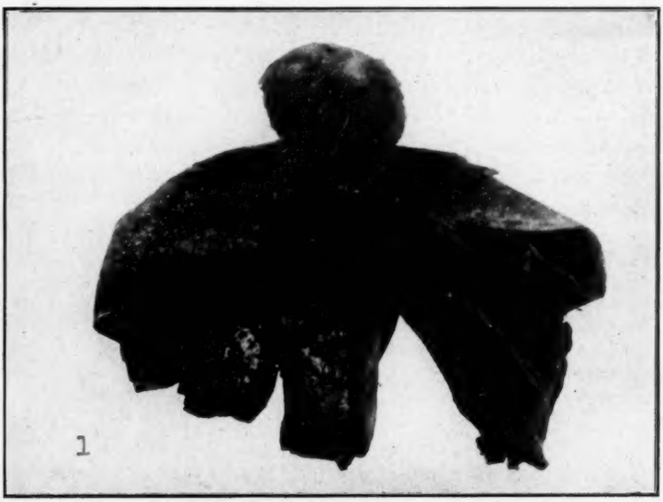

FIG. 1. *Trichaster melanocephallus* from Moravia.

about 4 cm. in diameter; *rays* sub-hygroscopic, unequal, acute, some of tips slightly revolute; *fleshy layer* 1–2 mm. thick, mummy brown (Ridgway), adnate, continuous; *exterior* naked, smooth, dark brown (russet), no signs of dirt or debris; *base* broad, concave with fragments of a cord-like rhizomorph in center. *Endoperidium* sessile, apparently globose before dehiscence, a few fragments left at base of gleba. *Gleba* subglobose, subsessile with a round thick, sub-ligneous stipe 1.5 cm. broad and expanding above into the regular gleba which is 2–3 cm. high by 2–3 cm. wide, consisting of spores, capillitium and columella; *columella* prominent, persistent, hard, sub-ligneous especially at the base, covered with a matted mass of capillitium and spores; *capillitium* thicker than

spores, 4.5–7 μ thick, walls thin, unbranched, contents tinted; *spores* 4.2–5.2 μ in diameter, globose; *epispore* chestnut brown, verrucose.

TYPE LOCALITY: Ukraine.

HABITAT: Solitary or in small groups on top of ground in deep forests.

DISTRIBUTION: Russia, Ukraine, *B. M. Czerniaiev,* many specimens at Kew, England & at Upsala, Sweden from type locality.

Moravia, Poullauerberge, May 1921, *Dr. J. Hruby,* under the name *Geaster fornicatus,* in F. Petrak, Flora Bohemiae et Moraviae Exsiccata no. 1498 (FIG. 1).

ILLUSTRATIONS: Lloyd, Myc. Writ. **1**: *pl. 17, f. 3.* Ed. Fischer in Engler and Prantl, Nat. Pfl. **7A**: *f. 53, A & B.*

The above description and photograph were made from the Moravian plant, listed above, with some additional data from the original description and from Lloyd's photograph of the type.

I can not find any generic differences between the genera *Trichaster* Czern. and *Geasteropsis* Hollós, both having caducous endoperidia and permanent sub-ligneous columellae. These are the only two characters that differentiate these genera from *Geaster,* and therefore *Geasteropsis* is made a synonym of *Trichaster;* however from the description and figures given by Hollós (l.c.) his *Geasteropsis Conrathi* seems to be different from *Trichaster melanocephalus.*

Trichaster Conrathi (Hollós) comb. nov. (FIG. 2)

Geasteropsis Conrathi Hollós, Novenyt. Kozlem. **2**: 72–75. 1903.

Sporophore epigeous, expanded at maturity to about 10 cm. in diameter; *exoperidium* revolute, thick, coriaceous, sub-hygrometric, splitting to about the middle into 10 unequal segments, concave below; *rays* irregular, curved; *exterior* ocher colored, brown and white variegated, longitudinally striate; *fleshy layer* adnate, brown, transversely fissured into corrugations. *Endoperidium* sessile, globose, whitish, soft, flexible, only fragments present which are adhering to the fleshy layer. *Gleba* stipitate, with an angular, stout, sub-ligneous stipe, 12 mm. wide at top, 20 mm. wide at base by 10 mm. tall, expanding above into the regular subglobose,

dark brown, gleba, 3 cm. in diameter, consisting of spores, capillitium and the sub-ligneous columella (FIG. 2). *Columella* firm, subglobose, persistent; *capillitium* subhyaline to dilute brown, rarely branched, non-septate, 4 μ in diameter, walls thick, lumen small; *spores* globose, 1-guttulate, some short pedicellate, 6–8 μ in diameter; *epispore* densely verrucose.

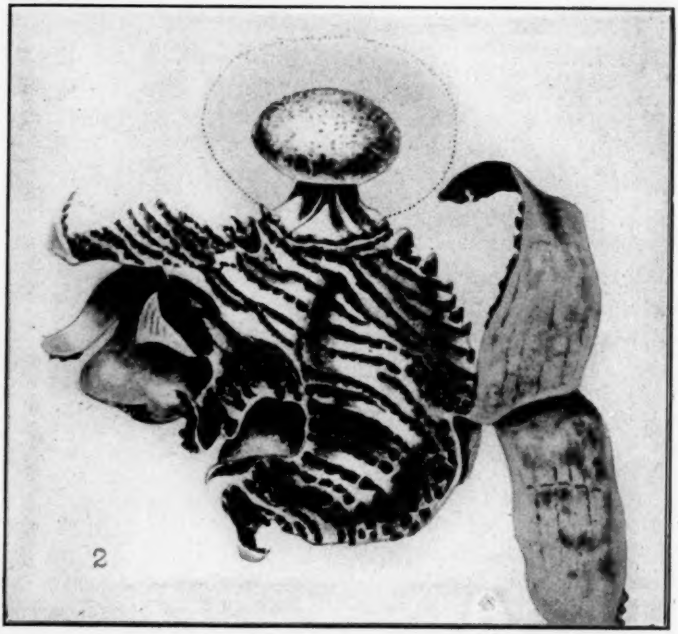

FIG. 2. *Trichaster Conrathi,* dotted circle former position of endoperidium (from Hollos) × 1.

HABITAT: In granitic soil on grassy slope, associated with *Welwitschia mirabilis* of the Gnetaceae.

DISTRIBUTION: Union of South Africa, Transvaal, 7½ miles from Johannesburg, elevation 4738 feet, *P. Conrath, 1 specimen,* type of *Geasteropsis Conrathi* Hollós.

ILLUSTRATIONS: Hollós, Novenyt. Kozlem. 2: *pl. 14, f. 1,* and *pl. 15, f. 2–3,* as *Geasteropsis Conrathi.*

The above description and figure were made from the original type description and figures by Hollós.

Ed. Fischer (**1933**) lists as a new species *Geasteropsis Stahelii,* but no adequate description or figure is given whereby this species can be identified and the name therefore becomes a *nomen nudum.*

Terrostella Long, nom. nov.

Geasteroides Long, Mycologia **9**: 271. 1917.

Peridium double; *exoperidium* splitting into stellate, reflexed, persistent segments; *endoperidium* fragile, upper portion more or less deciduous, lower part persistent, consisting of a prominent sterile base; *mouth* single; *columella* and *capillitium* present.

Terrostella texensis Long, comb. nov. (FIG. 3)

Geasteroides texensis Long, Mycologia **9**: 271. 1917.

Geasteropsis texensis (Long) Ed. Fischer in Engler & Prantl, Pfl. II, **7A**: 75. 1933.

Sporophore hypogeous, buttons not found but apparently acute, judging by the acuminate tips of the expanded exoperidium, becoming superficial and expanded at maturity, then 4–10 cm. in diameter, usual size 6 cm. *Exoperidium* revolute, thick, rigid, coriaceous, sub-hygroscopic, splitting to about the middle into 7–10 segments, concave below, convex above; *rays* unequal, recurved, with strongly involute, acuminate tips, 2–4 cm. long; *exterior* with an outer layer of arachnoid mycelium and dirt that peels off as the plants age, the exposed surface tilleul buff to dingy white, often with faint longitudinal striae; *fleshy layer* adnate, dark brown (carob brown), fissured and cracked when dry, gradually wearing away. *Endoperidium* short stipitate, subglobose, drab gray to light drab, 15–25 mm. broad by 18–20 mm. tall, very fragile, apparently with a poorly defined mouth, upper portion slowly dehiscing down to the sterile base, leaving it crowned with the subglobose columella and spores. *Sterile base* corky, compact, wood brown to fawn color, circular to oblong, circular ones 10–15 mm. across by 8–10 mm. tall, oblong ones 10 × 20 mm. to 25 × 27 mm. across by 10 mm. tall. *Stipe* terete to strongly flattened, stout, subligneous, 2–3 mm. thick by 3–15 mm. wide by 2 mm. high (tall). *Gleba* chestnut brown, in very old plants entirely disappearing and leaving only the sterile base seated on the stipe (FIG. 3); *columella* soft, weak, early deciduous; *capillitium* wine colored to light brown under the microscope, threads very long, distantly branched, 7–10 μ thick, tapering to a slender

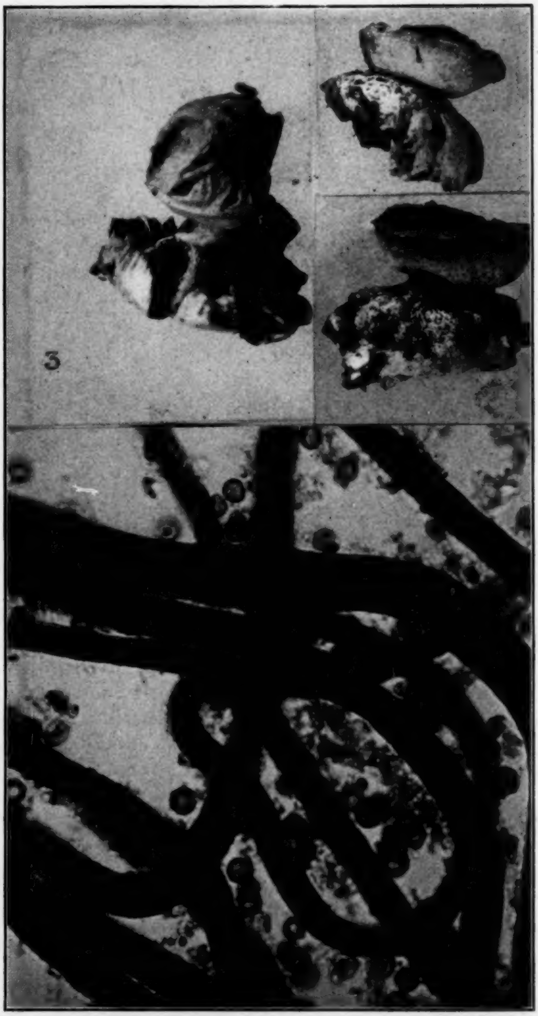

FIG. 3. *Terrostella texensis*, sporophores × 1; 4, *Terrostella texensis*, spores and capillitium, × 1000.

point, septate in thicker parts, breaking up into segments 800 to 1000 mμ long, walls smooth, often appearing as if filled with minute pits, lumen very small or none (FIG. 4); *spores* globose, 1-guttulate, 3–5 μ in diameter; *epispore* brown, 1 μ thick, faintly verrucose.

HABITAT: Solitary or in small groups, in rich loose, sandy loam around bases of old rotting post oak stumps (*Quercus stellata*) in open post oak woods.

DISTRIBUTION: Texas, Denton County, west of the Texas State Teachers College, Denton, elevation 620 feet, *W. H. Long*, September 28, 1906, *1671* (*4 plants*), October 8, 1907, *2011 Type* (*14 plants*), October 14, 1907, *2034* (*6 plants*); Pecan Creek near Denton, October 14, 1907, *2035* (*3 plants*).

These specimens were collected in three different localities in the vicinity of Denton; Nos. *2011* and *2034* were found 2 miles from the location of the first collection No. *1671*.

The distinguishing features of this species are its prominent, corky sterile base and its fragile deciduous endoperidium. Specimens are deposited as follows: 6 plants from type material in the Lloyd Myc. Col. No. *8787* as *Trichaster texensis*, a herbarium name; 4 plants from type material are in the Herbarium of the University of California at Berkeley, No. *53941*, under the name *Geasteroides texensis;* the remainder of the collections are in the Long Herbarium at Albuquerque, N. Mex.

The generic name *Geasteroides* is untenable since it is already preoccupied by Battarra's genus (**1755**) of same name, and especially since Ed. Fischer (l.c.) has revived this name as a synonym for *Geaster*. I am therefore changing the generic name of this fungus to *Terrostella* nom. nov.

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I am indebted to Mr. John A. Stevenson for the loan of material and many helpful suggestions and to Dr. David H. Linder for valuable suggestions on nomenclature.

ALBUQUERQUE, NEW MEXICO

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ADDITIONS TO THE UREDINALES REPORTED FOR PERU [1]

George B. Cummins

(with 5 figures)

The Uredinales reported in this paper were collected, for the most part, by Macbride and Featherstone and were made available for study by Dr. Francis Drouet, the Chicago Natural History Museum. All specimens are deposited in the Chicago Natural History Museum, with duplicates in the Arthur Herbarium of the Purdue University Agricultural Experiment Station. Species of rusts or of hosts marked with an asterisk are those not recorded by Garcia Rada and Stevenson (La Flora Fungosa Peruana. 112 pp. 1942. Lima, Peru).

***Aecidium mitoense** sp. nov.

Pycniis non visis. Aeciis hypophyllis, subepidermalibus, in greges minutos aggregatis vel plerumque sparsis, flavidis, 275–350 μ diam., cupulatis, margine recurvato; cellulis peridii flavidis oblongis, 17–24 × 49–68 μ, pariete exteriore minute verrucoso 4.5 μ cr., interiore 2 μ cr.; aeciosporae globoideae vel ellipsoideae, 18–23 × 22–31 (–35) μ; membrana 2.5–3.5 μ cr., minuteque verruculosa, flavida vel pallide aurea.

On *Sessea stipulata* R. & P., Mito, Peru, July 8–22, 1922, *Macbride & Featherstone 1487* (type). Alt. 9000 ft.

The aecia of this species characteristically occur rather widely scattered, frequently singly and seldom with more than a few sori in a group. Yellowish spots develop on the leaves where the aecia are grouped but they are usually small and inconspicuous. The long yellowish peridial cells are somewhat reminiscent of *Roestelia* but with finer markings than most species of that form-genus.

*Aecidium Fuchsiae Jacks. & Holw. *Fuchsia denticulata* R. & P., Muña, June 5–7, 1923, *Macbride 4285*.

[1] Journal Paper Number 217, of the Purdue University Agricultural Experiment Station. Contribution from the Department of Botany and Plant Pathology.

*AECIDIUM sp. *Baccharis alpina* H.B.K., Rio Blanco, Mar. 20–25, 1923, *Macbride 3024*. Alt. 15,000 ft.

This collection probably represents an undescribed species but it is too fragmentary to name. Aecia occur on the undersides of the leaves, evenly and closely scattered over the entire surface of all terminal leaves of a branch. This indicates that the infection is at least locally systemic whether perennial or not. The aecia are cupulate with an erose or slightly recurved margin, yellowish, and about 0.2 mm. in diameter. Aeciospores are globoid or occasionally ellipsoid, 17–19 × 19–23 (–25) μ with a yellowish, finely verrucose wall 1 μ in thickness.

*CEROTELIUM ? sp. *Halenia umbellata* (R. & P.) Gilg, Mito, July 8–22, 1922, *Macbride & Featherstone 1658*. Alt. 9000 ft.

This interesting but fragmentary specimen represents an undescribed species of questionable relationship. The rust is apparently microcyclic and devoid of pycnia. No species of similar morphology has been recorded on the Gentianaceae, nor have microcyclic species of unquestioned affinity been described in the genus *Cerotelium*.

Telia hypophyllous, subepidermal, densely gregarious in groups 3 mm. in diameter or up to 5 mm. in length along the midrib, individual sori, small, round 0.2–0.4 mm. in diameter, reddish and waxy in appearance becoming yellowish and somewhat farinaceous with maturity, 4–8 spores in thickness, without peridium or paraphyses; teliospores catenulate in origin but not firmly united either laterally or apically and therefore not in discrete strata or chains, oblong or ellipsoid, 10–15 × 22–32 μ (or smaller in immature condition); wall uniformly 1 μ or less in thickness, smooth, hyaline or essentially so.

CHRYSOCELIS LUPINI Lagerh. & Diet. *Lupinus *bogotensis* Benth., Huariaca, Apr. 3, 1923, *Macbride 3118; L. *humifusus* Benth., Mito, Aug. 1–5, 1922. *Macbride & Featherstone 1817; L. *mutabilis* Sims, Uspachaca, June 23, 1922, *Macbride & Featherstone 1301*.

*CHRYSOPSORA GYNOXIDIS Lagerh. (FIG. 1.) *Gynoxys* sp., Mito, Aug. 1–5, 1922, *Macbride & Featherstone 1842*.

The host was determined as *Sessea* but, because of the characteristic morphology of the rust, I am confident that the plant must be

a species of *Gynoxys*. It compares closely with specimens of *Gynoxys* in the Arthur Herbarium.

COLEOSPORIUM IPOMOEAE (Schw.) Burr. *Ipomoea *angulata* Lam., La Merced, Aug. 10–24, 1923, *Macbride 5340; I. purpurea* Lam., Huanuco, Apr. 5–8, 1923, *Macbride & Featherstone 3211,* Apr. 28, 1923, *Macbride 3532.*

KUEHNEOLA LOESENERIANA (P. Henn.) Jacks. & Holw. *Rubus *floribundus* H.B.K., Mito, July 8–22, 1922, *Macbride & Featherstone 1406; R. *roseus* var. *rosaeflorus* Hook., and var. *santarosensis* (Ktze.) Macbr., Muña, June 5–7, 1923, *Macbride 4287, 4289.*

MAINSIA HOLWAYI Jacks. *Rubus *bogotensis* H.B.K., Panao, May 10, 1923, *Macbride 3604; R. *floribundus* H.B.K., Mito, Aug. 10, 1922, *Macbride & Featherstone 1940; R. floribundus* var. **nimbatus* Mack., Yanahuanca, June 16–22, 1922, *Macbride & Featherstone 1219.*

PUCCINIA ABRUPTA Diet. & Holw. *Viguiera Pflanzii* Perkins, Mito, July 8–22, 1922, *Macbride & Featherstone 1535; V. *pusilla* (Gray) Blake, Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 471.*

***Puccinia abutiloides** sp. nov. (FIG. 2)

Pycniis, aeciis, et urediis nullis. Teliis subepidermalibus, hypophyllis, sparsis vel laxe aggregatis, rotundatis, usque ad 2.5 mm. diam., pulverulentis, cinnamomeo-brunneis vel obscurioribus, epidermide rupta plus minusve conspicue; teliosporae ellipsoideae, utrinque rotundatae, medio non vel vix constrictae, 23–29 × 33–45 μ; membrana uniformiter 3.5–4.5 μ crassa, cinnamomea vel pallide castanea, moderate verrucosa vel plus minus reticulato-verrucosa; poro superiore apicali, inferiore infra medium loculum sito; pedicello hyalino, fragili, brevissimo.

On *Abutilon virgatum* Sweet, Huanuco, Peru, Apr. 25, 1923, *Macbride & Featherstone 3494* (type). Alt. 7000 ft.

Telia of this species are paler brown, larger, and less inclined to occur in groups than is true of the telia of *Puccinia Abutili* Berk. & Br. The lower germ pore is close to the pedicel in both species and the size and shape of the spores are similar. However, the markings are conspicuously coarser in *P. abutiloides,* more irregular in shape and frequently are labyrinthiformly united or tend to

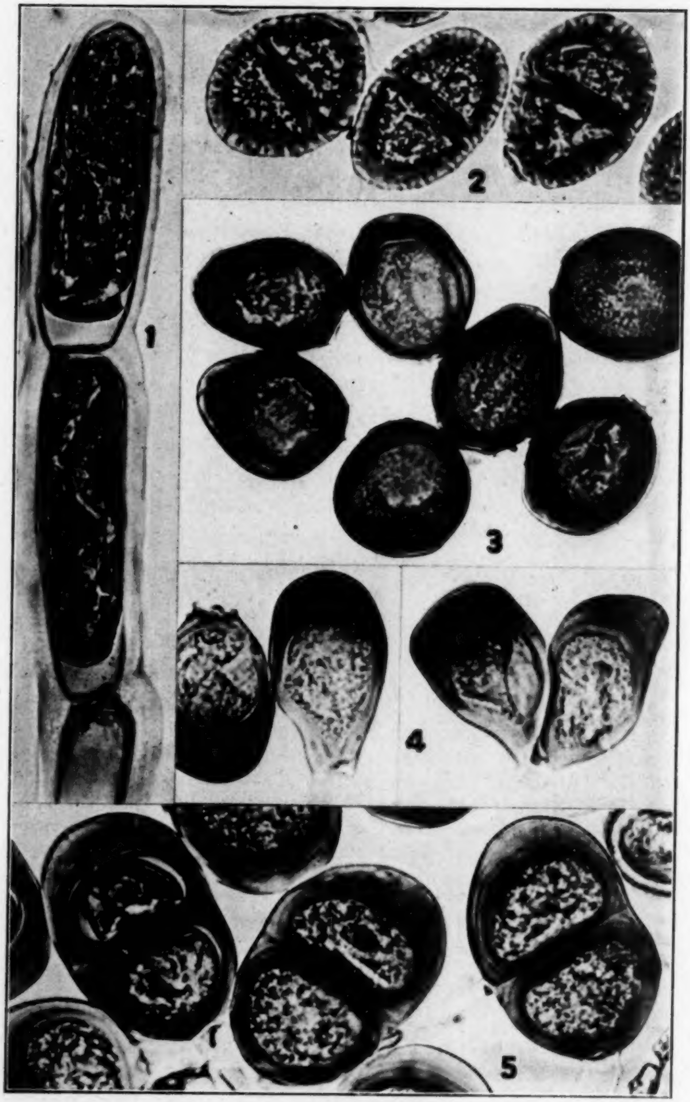


FIG. 1–5

occur in longitudinal lines. No American rust of Malvaceae is similar to *P. abutiloides*.

PUCCINIA ARISTIDAE Tracy. *Aristida adscensionis* L., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 341*.

*PUCCINIA BIMBERGI Mayor. *Heliopsis canescens* H.B.K., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 473a*.

*PUCCINIA BOMAREAE (Lagerh.) P. Henn. *Bomarea ovata* (Cav.) Mirb., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 353; B. tarmensis* Kränzl., Cueva Grande, June 23, 1923, *Macbride 4781*.

PUCCINIA CONOCLINII Seym. *Ageratum *conyzoides* var. *inaequipaleaceum* Hieron., Llata, Aug. 21, 1922, *Macbride & Featherstone 1997; Eupatorium *Kalenbornianum* Rob., Yanahuanca, June 16–22, 1922, *Macbride & Featherstone 1176, 1197,* San Rafael, Apr. 4, 1923, *Macbride 3135*.

*PUCCINIA CONTURBATA Jacks. & Holw.? *Salvia punctata* var. *glabra* Epl., Mito, July 8–22, 1922, *Macbride & Featherstone 1398, 1662*.

Both collections are meager. The rust is generally similar to *P. conturbata* but the germ pore in the lower cell of the teliospore is near the pedicel.

PUCCINIA CRASSICUTIS Syd. *Mutisia viciaefolia* var. *hirsuta* (Meyen) Wedd., Tarma, June 1–6, 1922, *Macbride & Featherstone 1015*.

*PUCCINIA DICHONDRAE Mont. *Dichondra repens* Forst., Chasqui, Apr. 10, 1923, *Macbride 3303*.

*PUCCINIA FESTATA Jacks. & Holw. *Euphorbia* sp., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 86*.

This species has been reported previously only from Ecuador.

PUCCINIA HETEROSPORA Berk. & Curt. *Anoda hastata* Cav., Llata, Aug. 21, 1922, *Macbride & Featherstone 1996*.

*PUCCINIA HIERACII (Schum.) Mart. *Hypochoeris sessiliflora* H.B.K., Rio Blanco, May 8–19, 1922, *Macbride & Featherstone 745*.

FIG. 1. Teleospore of *Chrysopsora Gynoxidis:* only the upper portion of the long, stout pedical is shown; 2, Teliospores of *Puccinia abutiloides* (from type); 3, Teliospores of *Uromyces Suksdorfii;* the spores are finely verrucose; 4, Teliospores of *Uromyces araucanus;* 5, Teliospores of *Puccinia Macbrideana* (from type), × 800.

*PUCCINIA IMPEDITA Mains & Holw. *Salvia occidentalis,* Huanuco, Sept. 23, 1922, *Macbride & Featherstone 2380.*

*PUCCINIA MINUSCULA Arth. *Helianthus Jelskii* Hieron., Yanahuanca, June 16–22, 1922, *Macbride & Featherstone 1199.*

The uredia in this collection have long, hyaline, thin-walled, cylindrical or clavate, peripheral paraphyses measuring 12–35 × 100–200 μ. When telia develop in old uredia they also have paraphyses but their presence could not be demonstrated in telia showing no urediospores. This may account for the fact that paraphyses are not mentioned in the original description or they may have been overlooked, since they can be confused with leaf hairs.

PUCCINIA MOGIPHANIS (Juel) Arth. *Alternanthera *calcicola* Standl., La Oroya, May 27–June 7, 1922, *Macbride & Featherstone 961; A. *porrigens* (Jacq.) Kuntze, Ambo, June 28, 1922, *Macbride & Featherstone 1348,* Huanuco, Apr. 26, 1923, *Macbride & Featherstone 3497.*

*PUCCINIA PUNCTATA Link. *Relbunium hypocarpium* (L.) Hemsl., Mito, July 8–22, 1922, *Macbride & Featherstone 1373.*

PUCCINIA ROSEANA Arth.? *Fourcroya *andina* Trel. and *F. *occidentalis* Trel., Matucana, Mar. 14–18, 1923, *Macbride 2923.*

A meager collection consisting of aecia.

PUCCINIA RUBIGO-VERA (DC) Wint. **Thalictrum podocarpum* H.B.K., Cuzco, Dec. 1928, *Herrera 1528a.*

*PUCCINIA SARACHAE Mayor. *Saracha biflora* R. & P., Cani, Apr. 16–26, 1923, *Macbride 3444.*

*Puccinia Satureiae sp. nov.

Pycniis subepidermalibus, epiphyllis, globoideis, 150–180 μ diam., paraphysatis. Aeciis subepidermalibus, hypophyllis, in greges usque 1.5 mm. diam. aggregatis, frequenter circinatim dispositis, flavidis, cupulatis, 150–185 μ diam.; cellulis peridii pallide flavidis, 17–26 × 36–45 (–60) μ, pariete exteriore 2 μ cr., interiore moderate verrucoso 4–6 μ cr.; aeciosporae late ellipsoideae vel ellipsoideae, 20–26 × 26–30 (–36) μ; membrana pallide flavida, 1.5 μ cr., moderate verrucosa. Urediis non visis verissimiliter nullis. Teliis hypophyllis, sparsis, pulvinatis, rotundatis, 0.1–0.3 mm. diam., aureo-brunneis; teliosporae oblongo-ellipsoideae vel plus minus cylindraceae, utrinque rotundatae, medio vix constrictae, 17–20 (–23) × 53–65 (–73) μ; membrana flavida, uniformiter 1 μ cr., levi; pedicello plus minusve sporam aequante, hyalino.

On *Satureia Pavoniana* Briq., Mito, Peru, July 8–22, 1922, *Macbride & Featherstone 1443* (type). Alt. 9000 ft.

Differentiated germ pores appear not to be formed. Germination of the teliospores occurs without a rest period. The basidium is formed at the apex of the upper cell and next to the septum in the lower cell.

PUCCINIA SHERARDIANA Körn. *Abutilon *sylvaticum* (Can.) Schum., Huacachi, May 20–June 1, 1923, *Macbride 4157.*

PUCCINIA SPILANTHICOLA Mayor. *Spilanthes ciliata* H.B.K., Huanuco, Apr. 28, 1923, *Macbride & Featherstone 3527.*

***Puccinia Macbrideana** sp. nov. (FIG. 5)

Pycniis et aeciis ignotis. Urediis amphigenis subepidermalibus, obscure cinnamomeo-brunneis, pulverulentis, sparsis, rotundatis vel ellipsoideis, usque 1 mm. longis, epidermide rupta conspicue; urediosporae late ellipsoideae vel ellipsoideae, $22–27 \times 28–35\,\mu$; membrana $2.5–3\,\mu$ cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 4–6, sparsis. Teliis amphigenis subepidermalibus, sparsis vel laxe aggregatis, frequenter plus minusve confluentibus, castaneo-brunneis, pulvinatis, rotundatis, 0.5–1.5 mm. diam.; teliosporae late ellipsoideae vel ellipsoideae, utrinque rotundatae, medio non vel vix constrictae, $29–40 \times 43–58\,\mu$; membrana castaneo- vel pallide castaneo- vel aureobrunnea, $3–5\,\mu$ cr., ad apicem $7–9\,\mu$, levi; poro superiore apicali, inferiore juxta septum sito; pedicello hyalino, usque ad $80\,\mu$ longo sed plus minusve fragili et frequenter deciduo.

On *Baccharis Sternbergiana* Steud., Llata, Peru, Aug. 21, 1922, *Macbride & Featherstone 1992* (type). Alt. 7000 ft.

Puccinia Macbrideana has a general resemblance to *P. unicolor* Arth. but has larger telia, somewhat larger teliospores whose walls are darker in color, and uredia which are dark brown and much larger. The urediospores, too, differ strikingly from those of *P. unicolor* because of their cinnamon-brown color, thick walls, and coarser echinulation. Germ pores in the urediospores are covered with slight cuticular umbos and while relatively large are not readily observable.

PUCCINIA sp. *Geum?* sp., Muña, trail to Tambo de Vaca, June 5–7, 1923, *Macbride 4316.*

Uncertainty concerning the identity of the host and the meagerness of material make it impossible to do more than record the characteristics of this rust.

Pycnia epiphyllous, subepidermal, few in a group, depressed globoid or lenticular, 135–165 µ wide, 60–90 µ high, with short and inconspicuous paraphyses. Aecia mainly epiphyllous, subepidermal, without paraphyses, uredinoid, circinately confluent in a ring, 1–1.5 µ in diameter, around the pycnia, yellowish, pulverulent, ruptured epidermis conspicuously elevated; aeciospores mostly ellipsoid, 19–25 × 29–35 (–37) µ; wall hyaline or pale yellowish, 2–3 µ thick, echinulate with stout spines 2–2.5 µ long; pores obscure, perhaps equatorial. Uredia not distinguished with certainty, if present differing from the aecia only in the scattered distribution and hypophyllous position. Telia hypophyllous, scattered, pulvinate, chestnut-brown, round, 0.2–0.4 mm. in diameter; teliospores somewhat variable but mostly ellipsoid or clavate-ellipsoid, rounded at the apex, rounded or narrowed at the base, slightly constricted at the septum, 25–31 (–35) × 42–55 (–59) µ; wall 2 µ thick at sides, light chestnut-brown, thickened to 4–7 µ over the pores by a semihyaline umbo, finely and evenly verrucose; germ pore apical in the upper cell, next the septum in the lower cell; pedicel hyaline or yellowish, thin-walled, about as long as the spore, mainly persistent. The teliospores germinate without a period of rest.

***Uredo Arcytophylli** sp. nov.

Urediis subepidermalibus, hypophyllis, pulverulentis, cinnamomeis, sparsis, ellipsoideis, 0.3–0.8 mm. longis, epidermide rupta conspicue; urediosporae late ellipsoideae, ellipsoideae vel oblongo-ellipsoideae, 19–25 (–29) × 29–33 (–36) µ; membrana 1.5–2 µ cr., cinnamomea vel pallide cinnamomea, minuteque echinulata; poris 6–8, plus minusve obscuris.

On *Arcytophyllum thymifolium* (R. & P.) Standl., Tarma, Peru, June 1–6, 1922, *Macbride & Featherstone 1013* (type). Alt. 7000 ft.

The pores are difficult to observe with accuracy but usually occur more or less in the equatorial region but not in distinct bands. There are apparently three or four one side of the spore and an equal number on the opposite side, the spores somewhat flattened on the pore-bearing sides.

UREDO IRREQUISITA Jacks. & Holw. *Verbesina *Sodiroi* Hieron., Chinche, June 21, 1922, *Macbride & Featherstone 1257.*

*UREDO sp. *Manettia peruviana* Standl., Mito, July 8–22, 1922, *Macbride & Featherstone 1442.*

Uredia in this specimen are amphigenous and cinnamon-brown, the spores obovate with the base rather broad, 24–27 × 27–33 μ, the wall moderately echinulate, 1.5 μ thick, cinnamon-brown, and provided with two basal pores. The collection may possibly be referable to *Goplana andina* Syd. described on *Manettia Lobbii* from Ecuador. Germ pores in *G. andina* are described as obscure.

UREDO sp. *Alternanthera elongata* (Willd.) Schinz., San Rafael, Apr. 4, 1923, *Macbride 3139.*

While similar macroscopically to the uredia of *Puccinia mogiphanis* (Juel) Arth. this rust differs in having closely echinulate spores with three strictly equatorial pores. *Uredo Alternantherae* Jacks. & Holw. has echinulate spores but scattered pores. Spores in the above collection measure 26–30 × 30–35 μ, with a cinnamon-brown wall 2.5 μ thick.

*UROMYCES ARAUCANUS Diet. & Neger. (FIG. 4.) *Senecio* sp., Yauli, May 25, 1922, *Macbride & Featherstone 923.* Alt. 13,500 ft.

No material has been available for comparison and this collection is identified with *U. araucanus* with uncertainty. The sori occur in confluent groups 2–5 mm. in diameter, the individual sori early merging to form a continuous sorus, chestnut-brown, compact, and only loosely covered by the ruptured and somewhat shredded epidermis. Such characteristics do not agree well with the description of *U. araucanus.* The spores appear to be similar, measuring 20–27 × 33–43 μ, with an occasional spore much larger. The wall is chestnut-brown, 2–3 μ at the sides and 6–9 μ at the apex. Pedicels are hyaline rather than brownish as in *U. araucanus.*

UROMYCES BIDENTICOLA (P. Henn.) Arth. *Bidens *leucanthema* (L.) Krause, Huanuco, Sept. 23, 1922, *Macbride & Featherstone 2318a; B. pilosa* var. *dubia* (Cass.) O. E. Schulz, Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 170.*

*UROMYCES COMMELINAE (Speg.) Cooke. *Tradescantia cymbispatha* Clarke, Mito, July 8, 1922, *Macbride & Featherstone 1616.*

*UROMYCES CUCULLATUS Syd. *Baltimora recta* L., La Merced, Aug. 10–24, 1923, *Macbride 5456.*

*UROMYCES ERAGROSTIDIS Tracy. *Eragrostis pilosa* (L.) Beauv., Apr. 12–May 3, 1922, *Macbride & Featherstone 394.*

*UROMYCES HEDYSARI-PANICULATAE (Schw.) Ellis. *Desmodium uncinatum* (Jacq.) DC., Cabello, June 25, 1922, *Macbride & Featherstone 1332.*

UROMYCES LATHYRINUS Speg. **Vicia Matthewsii* Gray, Rio Blanco, Mar. 20–25, 1923, *Macbride 2964.*

UROMYCES PROËMINENS (DC.) Pass. *Euphorbia *geniculata* Ortega, Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 274; E. lasiocarpa* Kl., Rio Huallaga Cañon, June 3, 1923, *Macbride 4231; E. *rhytisperma* Engelm., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 201.*

*UROMYCES SPHAERICUS Jacks. & Holw. *Perymenium ecuadoricum* Blake, Huanuco, Apr. 28, 1923, *Macbride & Featherstone 3525.*

UROMYCES STRIATUS Schroet. *Medicago *lupulina* L., Mito, July 8–22, 1922, *Macbride & Featherstone 1558.*

*UROMYCES SUKSDORFII Diet. & Holw. (FIG. 3.) *Silene chilensis* (Gay) Cham. & Schlecht., Rio Blanco, Mar. 20–25, 1923, *Macbride 2962.*

This specimen, collected at an altitude of 15,000 ft., has more finely verrucose teliospores than most previous collections but is undoubtedly too closely related to segregate as a species. *U. Suksdorfii* has not been reported previously south of the United States.

*UROMYCES TENUISTIPES Diet. & Holw. *Desmodium mollicula* (H.B.K.) DC., Mito, July 8–22, 1922, *Macbride & Featherstone 1371.*

*UROMYCES TRIFOLII-MEGALANTHI (Diet. & Neger) Jacks. & Holw. *Trifolium peruvianum* Vog., Rio Blanco, May 8–19, 1922, *Macbride & Featherstone 750.*

THE ARTHUR HERBARIUM,
PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION,
LAFAYETTE, INDIANA

TWO NEW GENERA OF RUSTS ON BIGNONIACEAE

B. B. Mundkur and M. J. Thirumalachar

(with 8 figures)

A rust on *Stereospermum suaveolens* was placed in the genus *Phakopsora* by Mundkur (**1943**) who claimed that he had found the aecial stage which, until then, was unknown for the genus. A re-examination of the rust has now revealed that what he claimed to be aecia are merely the immature stages of the telia and that the rust itself does not fit into the genus *Phakopsora*. A new genus has been established to accommodate the rust and named *Mehtamyces,* for Dr. K. C. Mehta, a distinguished Indian Cereal Rust Pathologist.

The rust is a hemiform with pulverulent, subepidermal uredia. Dr. G. B. Cummins of the Arthur Herbarium to whom a specimen was sent wrote to say that the uredia and the urediospores closely resemble and in fact are identical with those of *Uredo Stereospermi* Sydow, recorded on *Stereospermum chelonoides* (L.f.) DC. He also wrote that the rust did not appear to him to be a typical *Phakopsora* and suggested that a new genus may have to be established for its accommodation.

This re-examination has confirmed that view. Bits of the herbarium material were softened for a detailed microtome study and good sections were obtained. They were stained with safranin using light green as counter-stain. The material is very old, still the degenerated nuclei within the teliospores could be made out. There were two of them in the young teliospores and a single fusion nucleus in the mature ones.

The urediospores are pedicellate and are formed in clusters on sporogenous basal cells. This feature has already been pointed out by Cummins (**1940**) for *Uredo Stereospermi.* The development of urediospores in clusters on sporogenous basal cells, the

presence of bilaminate wall with bicapitate apex strongly suggest the characters of the genus *Prospodium.* That genus is, so far as it is at present known, confined to the Western Hemisphere and Cummins did not, in the absence of the telial stage, transfer *Uredo Stereospermi,* a step which was very wise.

The telia, which distinguish the rust from *Prospodium,* are subepidermal and non-erumpent, the infection patches being circular to irregular in outline, slightly raised and black and up to 3 cm. in diameter. Sections through the telia indicate that they are mostly epiphyllous, very rarely amphigenous. The sori (FIG. 1) are formed between the epidermis and the palisade layers by the concentration of the hyphae. The sorus is not limited in outline as it becomes indefinite by the confluence of the infection patches. The teliospores are formed from the base of the sori in regular chains. The young spores are rectangular, thin-walled, somewhat hyaline, showing two distinct nuclei (FIG. 2), which on account of the age of the specimens present a shrivelled appearance. Mature spores are cuboid to rectangular (FIG. 3), yellowish-brown, smooth and measure $13–33 \times 8–15\,\mu$. Immature telia resemble caemoid aecia that have not erupted, which led Mundkur (**1943**) into an error. Mature spores get dispersed by the disintegration of the host tissue.

The occurrence of subepidermal uredia and of urediospores borne in clusters on sporogenous cells, taken along with telia which occur in subepidermal non-erumpent crusts with teliospores in regular chains, indicates that the rust cannot be accommodated in any of the rust genera so far described. In the type of uredia and of urediospores it completely resembles species of *Prospodium* in possessing clustered urediospores whose wall is bilaminate with a bicapitate apex. The telia themselves to a certain extent resemble the telia of *Angiopsora* in having catenulate teliospores but differ in not being lenticular; in fact they are definite. These combinations of characters justify the erection of the genus *Mehtamyces.*

Mehtamyces gen. nov.

Pycnia and aecia unknown. Uredia subepidermal, aparaphysate; urediospores borne in clusters on sporogenous basal cells; walls bilaminate. Telia in subepidermal crusts, non-erumpent,

indefinite; teliospores developed in chains, basipetally; germination unknown.

Type species: *Mehtamyces Stereospermi* (Mundkur) Mundkur & Thirumalachar.

Pycnia atque aecia ignota. Uredia subepidermalia, aparaphysata; uredosporae catervatim ortae ex sporogenis basicis cellulis, parietibus bilaminatis. Telia in crustis subepidermalibus, haud erumpentia, indefinita; teliospora catenatim basim versus productae; germinatio ignota.

Species typica; *Mehtamyces Stereospermi* (Mundkur) Mundkur et Thirumalachar.

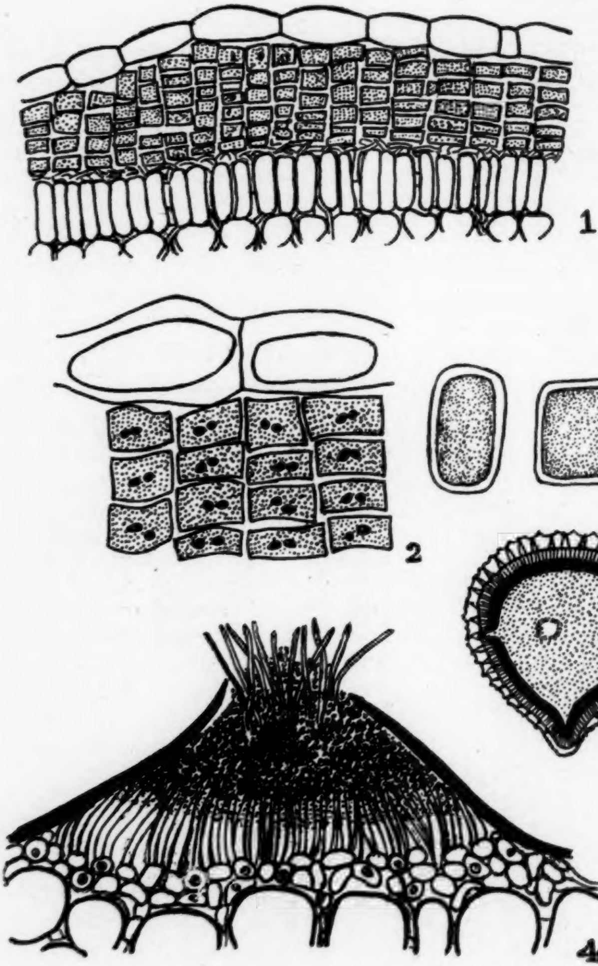
Mehtamyces Stereospermi (Mundkur) comb. nov.

Uredo Stereospermi Sydow, Ann. Myc. **13**: 37. 1915.
Phakopsora Stereospermi Mundkur, Mycologia **35**: 542. 1943.

Uredia amphigenous, mostly hypophyllous, sparse, pale-yellowish brown; urediospores obovate-ellipsoid, with two approximately equatorial germ pores, 24–35 × 19–25 μ; inner wall yellowish, up to 2 μ thick, outer phaline and hygroscopic, up to 7 μ thick, investing the spores in the form of a band between the pores and being bicapitate at apex; sparsely echinulate. Telia circular to irregular in outline, black, slightly raised, indefinite, non-erumpent, aparaphysate; teliospores in chains of 4 to 8 spores, formed between the epidermis and palisade layers, yellowish brown, rectangular to cuboid, 13–33 × 8–15 μ; wall up to 2.5 μ thick.

On living leaves of *Sterospermum suaveolens* Wall. Nagpur (Central Province), 17–9–1922, coll. R. T. Pearl (Type); type deposited in *Herb. Crypt. Ind. Orient.*

In 1943 Rev. Father H. Santapau, S.J., Professor of Botany, St. Xavier's College, Bombay, collected a rust on *Heterophragma Roxburghii* at Khandala, near Poona. The rust occurs in great abundance in the Western Ghats and field observations by Father Santapau have shown that affected trees are severely defoliated. One tree growing in the Government Botanic Garden at Bangalore also showed severe infection and afforded an opportunity for watching the various stages in the life cycle of the rust. For morphological study the material was fixed in formalin acetic alcohol and the microtome sections were stained with Newton's iodine gentian violet.



FIGS. 1–5. *Mehtamyces Stereospermi.*

The rust is an autoecious eu-form occurring throughout the year, mostly in the uredial stage. The leaves are completely covered over their surface by the pustules and the powdery masses of urediospores form clouds of dust when the trees are violently shaken.

The pycnia (FIG. 4) are formed soon after the telial stage is over in the month of December. Leaves bearing the telia drop to the ground and when collected the next morning, after a heavy dew fall, show abundant teliospore germination. The sporidia infect the young, newly formed leaves of the host and the infection spot appears as a crimson yellow speck, gradually becoming swollen and pulvinate. By about the tenth day, numerous pycnia develop in concentric rings on both sides of the infection spot. Pycnia are amphigenous, subcuticular, conoid and slightly compressed. A few ostiolar filaments emerge but they are embedded in nectar containing numerous pycnospores. Nectar is secreted in copious quantities.

The aecia (primary uredia) soon replace the pycnia and are uredinoid (FIG. 6). They are mostly epiphyllous and only occasionally amphigenous, subcuticular, erumpent and pulverulent. Due to the confluence of the infection patches, the sori become indefinite. From the base of the sori binucleate hyphae which are cylindric emerge out, breaking through the cuticle. From their tips are formed the young aeciospores which resemble the urediospores. Mature spores are obovate to ellipsoid with a bilaminate wall. The inner wall is golden brown, up to 5 μ thick; the outer wall is hyaline, hygroscopic, forming a band on one side, thus resembling the unicapitate type of spores of some species of *Prospodium*. Three distinct germ pores situated about the equator can be observed. The aeciospores germinate readily when placed in drops of water in a moist chamber.

The uredia (secondary uredia) follow the aecia in development. They are also amphigenous, and can be differentiated from the aecia by their subepidermal nature (FIG. 7). The uredial initials are formed beneath the epidermis and, as development takes place, stipitate urediospores borne singly on pedicels are formed, which resemble the aeciospores (FIG. 5). Even though little difference exists between the aeciospores and the urediospores, still the aecia

are always associated with the pycnia whereas the uredia are grouped with the telia.

The telia are formed only between the months of September and December. The telia are amphigenous, subepidermal and erumpent. Mature telia occur as waxy rusts, the spores being formed in regular chains which on rupturing appear as short columns (FIG. 8). The mature telium becomes slightly pulverulent at the apex as in *Cerotelium* and the spores also show a tendency to get separated. In a young telium the binucleate cells organize themselves as subepidermal crusts and they very much resemble the telial crusts of *Melampsora*. Very soon more spores are abstricted basipetally and in chains which coalesce laterally to form short columns. Mature spores are hyaline to pale cinnamon yellow, with a prominent fusion nucleus which can be seen in stained preparations.

The type of structure and the manner of development of the teliospores in this rust closely resemble the condition present in the genus *Cerotelium*. According to Mains (**1921**) the genus *Cerotelium* includes those rusts alone which have subepidermal uredia lined with a peridium or hyphoid paraphyses and sessile urediospores and telia that are also subepidermal, slightly columnar, containing catenate teliospores with lateral coalescence, later becoming pulverulent and germinating away at the apex. In *Kuehneola,* on the other hand, the urediospores are stipitate and the telia consist of catenate teliospores but the chains remain free right up to the base.

The rust on *Heterophragma Roxburghii* has the characters mentioned above for the genus *Cerotelium* so far as the structure of the telium and the type of germination are concerned. But when the other spore-forms are taken into consideration, differences begin to manifest themselves. The pycnia are no doubt subcuticular both in *Cerotelium* and the present rust but the lack of ostiolar filaments is stressed as an important character for *Cerotelium* whereas they are quite conspicuous in the present rust. The aecia are cupulate and peridiate. *Cerotelium Dicentrae* (Trelease) Mains who first (**1921**) described the aecial stage for the genus, whereas they are subcuticular and uredinoid in the *Heterophragma*-rust. The lack of a peridium or hyphoid paraphyses in

the uredia, as well as the pedicellate nature of the urediospores of the latter rust, indicates that the rust belongs to a separate genus. Subepidermal crusts of telia with teliospores developing in chains are known in *Angiopsora, Dasturella* and the rather imperfectly known Bignoniaceous rust *Uropeltis.* The genus *Angiopsora* is separated from *Phakopsora* only in having teliospores in chains. But in both the genera the telia are non-erumpent and the teliospores are resting spores. In *Dasturella,* which has erumpent telia, they are in the form of flabelliform crusts and the teliospores are also resting spores and do not germinate as soon as they mature as in the *Heterophragma*-rust. The combination of characters found in this rust necessitates therefore the erection of a separate genus for its accommodation. The name *Santapauella,* for Rev. Father Santapau, is proposed for it.

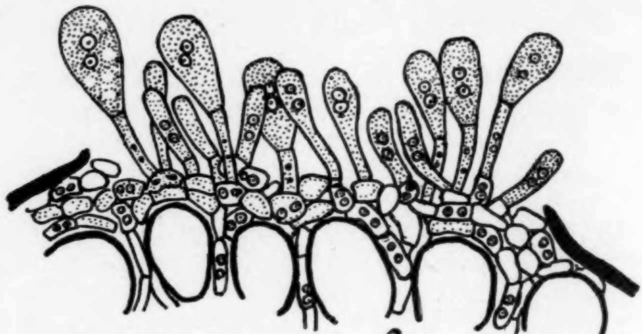
The genera *Mehtamyces* and *Santapauella* can be differentiated among themselves on the basis of the following characters. In both the uredia are subepidermal but the urediospores are borne in clusters on sporogenous basal cells in the former and singly on pedicels in the latter. The hyaline hygroscopic sheath forming the outer layer in both the genera is reminiscent of *Prospodium* but the apex is bicapitate in *Mehtamyces* and unicapitate in *Santapauella.* In *Mehtamyces* the telia are not erumpent, and the teliospores which are formed as crusts within the leaf tissue are resting spores. As against this, in *Santapauella* the telia are erumpent, develop as short columnar crusts and tend to become pulverulent and germinate away at the apex as soon as they are mature.

Santapauella gen. nov.

Pycnia subcuticular; aecia uredinoid, subcuticular and aparaphysate; uredia suberpidermal, aparaphysate, with pedicellate spores borne singly on pedicels; telia in subepidermal crusts, erumpent, pulverulent at apex; teliospores catenate, hyaline, germinate without a rest period.

Type species: *Santapauella Heterophragmae* Mundkur & Thirumalachar.

Pycnia subcuticularia. Aecia uredinoidea, subcuticularia, aparaphysata. Uredia subepidermalia, aparaphysata, ornata, sporis pedicellatis, quarum



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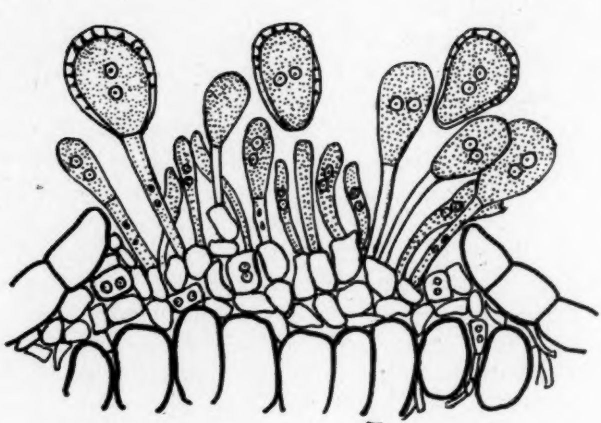

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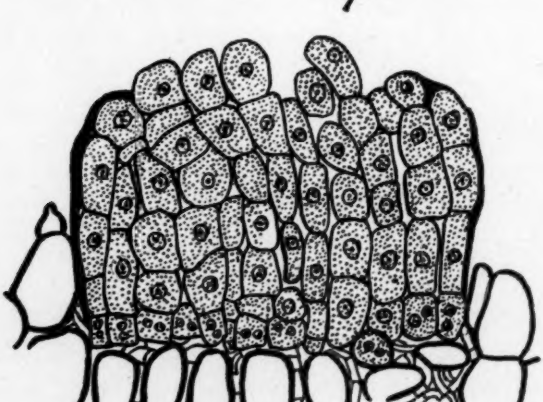

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FIGS. 6–8. *Santapauella Heterophragmae.*

singulae pediculo insident. Telia in crustis subepidermalibus, hyalinae, germinantes absque ulla quietis mora.

Species typica: *Santapuella Heterophragmae* Mundkur & Thirumalachar.

Santapauella Heterophragmae sp. nov.

Pycnia conoid, broader than long, sometimes compressed, with ostiolar paraphyses 220 to 330 μ broad and 100–155 μ high; pycniospores hyaline to pale yellow. Aecia erumpent, indefinite because of coalescence; aeciospores resembling urediospores, measuring 24–32.5 × 20–27 μ. Uredia amphigenous, erumpent, pulverulent; urediospores, borne singly on pedicels, obovate to ellipsoid, sparsely echinulate, measuring 24–32 × 20–27 μ; with three approximately equatorial germ pores; wall bilaminate, inner golden yellow up to 5 μ thick; outer hyaline, hygroscopic, forming a band on one side, appearing to be unicapitate. Telia amphigenous, aparaphysate; teliospores in chains with 7 to 10 spores per chain, chains coalescing laterally, hyaline to pale cinnamon yellow, smooth, without distinct pores at maturity, measuring 11–19 × 9–17 μ; germnation as soon as teliospores are mature, starting at apex.

On living leaves of *Heterophragma Roxburghii* DC. Khandala (Bombay), 13–6–1943, coll. H. Santapau (No. 2207); Lalbagh, Bangalore (Mysore), 8th September, 1944, coll. M. J. Thirumalachar & B. B. Mundkur (type); deposited in the Herb. Crypt. Ind. Orient.

Santapauella Heterophragmae sp. nov.

Pycnia conoidea, latitudine praestantiora quam longitudine, nonnumquam compressa filamentis ostiolaribus; pycniosporae hyalinae ad pallide luteas. Aecia erumpentia, ob coalescentiam indefinita; aecisporae urediosporis similes, magnitud. 24–32.5 × 20–27 μ. Uredia amphigena, erumpentia, pulverulenta; urediosporae singulae pediculis insidentes, obovatae ad ellipsoideas, sparse echinulatae, magnit. 24–32 × 20–27 μ; tribus germinationis poris plus minus equatorialibus ornatae; parietes duplices, quorum interior luteus, ad 5 μ crassus; exterior hyalinus, hygroscopicus, vittam in latere efformans atque unicapitatus apparens. Telia amphigena, aparaphysata; teliosporae catenatim dispositae (7–10 sporis in singulis catenis, quae lateraliter coalescunt), hyalinae ad cinnamomo-luteas, leves, absque distinctis germinationis poris in maturitate, magnitud. 11–19 × 9–17 μ; germinant statim ac teliosporae ad maturitatem perveniunt, ab apice incipientes.

In foliis viventibus Heterophragmae Roxburghii DC. Khandala (Bombay), 13–6–1943, legit H. Santapau; Bangalore (Mysore), 8–9–1944, leg. M. J. Thirumalachar et B. B. Mundkur (typus).

We wish to express our deep debt of gratitude to Rev. Father Santapau for his kindness in placing at our disposal his collection of rust on *Heterophragma Roxburghii* and for rendering into Latin the diagnoses of the new genera and species and to Dr. G. B. Cummins for drawing our attention to some of the salient points in the life history of the above rusts.

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EXPLANATION OF FIGURES

Mehtamyces Stereospermi

1. Section through the telium showing development between epidermis and palisade layers. × 400.
2. Enlarged view showing chains. × 900.
3. Mature teliospores. × 1020.

Santapauella Heterophragmae

4. Subcuticular pycnium. × 720.
5. Urediospore showing bilaminate wall and germ pores. × 900.
6. Uredinoid aecium. × 400.
7. Uredium. × 400.
8. Telium showing erumpent columns. × 400.

FURTHER REMARKS ON MYCOGENETIC TERMINOLOGY

B. O. Dodge

HETEROCARYOSIS AND HETEROSIS

When race "yellow dwarf 16" of *Neurospora tetrasperma* was grown in "mixed culture" with race C_4, nuclear migrations occurred so that a heterocaryotic mycelium was soon built up (Dodge, **1942**). This mycelium then grew with great vigor. It was pointed out that we had here a phenomenon analogous to hybrid vigor in diploid plants and animals. Since a heterocaryotic haploid mycelium is in no sense hybrid, the phrase heterocaryotic vigor was suggested to characterize the phenomenon. One frequently finds in recent literature statements such as "hybrid vigor or heterosis," implying that the two expressions are synonymous. Whaley (**1944**), however, has reminded us that this is an erroneous use of the term heterosis since Shull (**1914**) defined it as the "stimulus of heterozygosis," the "stimulating effects of hybridity" or "the stimulation due to the differences in uniting gametes." According to Shull, then, hybrid vigor is the *manifestation* of the effects of heterosis which in turn is the *stimulus* of heterozygosis. All three terms apply to diploid organisms, although those having more than the 2n number of chromosomes might very well show hybrid vigor, that is, if they are heterotic hybrids.

It is obvious that it would be incorrect to say that heterocaryotic vigor is one form of heterosis. Hanson and Smith (**1932**) were fully aware that dicaryotic and heterocaryotic mycelia are not hybrid diploid structures when they first suggested the term "heterocaryosis" to cover situations where two or more genetically different kinds of nuclei are operating in the same cells or in the same cytoplasm. Heterocaryosis should be compared to heterozygosis and not to heterosis. There is at present no mycogenetic

term comparable to heterosis. One can say, however, that heterocaryotic vigor is the manifestation or the effects of the stimulus of heterocaryosis. At the time when Shull (**1914**) defined "heterosis" the phenomenon heterocaryotic vigor had not been recognized as such. From conversations and correspondence with that author we must believe that had this phenomenon been known he would have broadened his concept of heterosis to include stimuli of heterocaryosis.

The writer's associates Dr. W. J. Robbins and Dr. H. W. Rickett on being approached on this point suggested that the word "choriheterosis" could be used to signify the stimulus of heterocaryosis, and "synheterosis" to signify the stimulus of heterozygosis. The following chart may serve to bring out the relationship of two comparable sets of terms.

Haploid organisms		Diploid organisms
1.[1] Heterocaryotic vigor		1a. Hybrid vigor
	(Heterosis)	
2. Choriheterosis		2a. Synheterosis
3. Heterocaryosis		3a. Heterozygosis

[1] Nos. 1 and 1a refer to manifestations;
Nos. 2 and 2a refer to stimuli;
Nos. 3 and 3a refer to spatial or organic relationships of the genes involved.

There would be no point in using the term heterosis, as some have done, to mean hybrid vigor which is such an expressive phrase and one that can not be improved upon. Much has been written on the causes of hybrid vigor and the stimulus of hybridity. If an equal amount of research by equally well equipped investigators were devoted to heterocaryotic vigor and the effects of heterocaryosis we might come to a better understanding of hybrid vigor. For this work the facultatively heterothallic ascomycetes such as *Neurospora tetrasperma* would serve most admirably.

HETEROTHALLISM AND HAPLODIOECISM

It was not possible to include in a recent note on terminology (Dodge, **1945**) an extended discussion of heterothallism. Jackson

(**1944**) made the very good point that Blakeslee's (**1904**, **1906**) definition of this term carried with it "a definite implication with reference to the separation of the sexes in different thalli." When one reads only those two papers one must agree with Jackson, especially in view of the fact that in plate 6 (Blakeslee, **1906**) the symbols ♀, ⚥ and ♂ were used exclusively instead of the symbols + and −. Certainly it does look as though femaleness and maleness were uppermost in his mind, plus (+) being female and minus (−) being male. Even in some of his later papers the same idea was more or less emphasized, but more from the biochemical standpoint. However, if one rereads all his papers on sex one must be convinced that we have not gradually come to apply the terms heterothallism and homothallism in an entirely different way from that which their author intended forty years ago.

Heterothallism does imply the segregation of factors which control sex-reactions or which determine mating types. It is genotypic and does not imply phenotypic, morphological sex-differentiations. An example will be cited later showing that rarely the two types of differentiation may possibly operate in a closely linked fashion.

Blakeslee's "type material" which served as the basis for his new term heterothallism was, no doubt, the "Harvard strain" of *Rhizopus nigricans*. This he found, to the consternation of many conservative teachers of botany, was really a mixture of two different strains, neither of which could produce zygospores by itself. Individual spores from a sporangium were not totipotent. There were no constant differences morphologically between the two progametangia which united to form zygospores in fertile cultures. Nevertheless, the two races which united to bring about sexual reproduction were genotypically of opposite sex. All heterothallic species of the Mucoraceae are like *Rhizopus* in the three respects circumscribing heterothallism, as noted above. Haplodioecism should, as other authors have pointed out, be reserved for those haploid organisms which do have two kinds of thalli, "male" and "female" thalli which can be distinguished morphologically. A few quotations from Blakeslee's papers support the above conclusions.

He says (**1906**, p. 163), "That as yet it has not been possible to substitute the terms male and female for (+) and (−) or *vice versa,* does not in the least detract from the conclusion, however, that the differentiation is a sexual one." Page 175 of the same paper, he says, "A heterothallic condition on the other hand can never be recognized by a morphological investigation alone."

In his retiring Vice-presidential address Blakeslee (**1920**, p. 377) says also, "In a considerable number of races in several species, however, I have found that the plus race is not invariably more vigorous than the minus when a difference in vegetative vigor is observed, judging vigor by former criteria; but this fact does not detract in the least from the evidence that in the plus and minus races we have two sexes represented." Farther on, "The main point to be brought out is that dioecious mucors are not to be homologized with dioecious flowering plants and higher animals. More nearly are the sexual races of mucors to be compared with the gametes themselves of such higher plants and animals." Notice he says in the last sentence *"more nearly"* and not "exactly"! In the same address he says of the sex reactions of *Zygorhynchus heterogamus,* "they serve to call attention to the fact that those who define male and female in terms of size differentiation in sex cells are making the gratuitous assumption that quantitative differences in the gametes are the fundamental peculiarities of the two sexes. I have used from preference, therefore, the terms plus and minus because I wish to speak in terms of physiological differentiation into sexually dimorphic races established in dioecious species rather than in terms of male and female which are defined by differentiation in size of gametes and which conceivably may be secondary sex characters."

In certain species of the Florideae the thalli are of two sorts, carpogonial and antheridial. Such thalli are often referred to as female and male plants. Many red algae are bisexual or hermaphroditic. It is strange that Blakeslee should have failed to cite such examples if he really had this type of femaleness and maleness in mind when he defined heterothallism and referred to the thalli of opposite sex as + and − thalli.

Much more to the point is his omission of the haplodioecious species of the Laboulbeniales. Working in close association with

Thaxter who described a dozen or so "dioecious" genera with numerous species, Blakeslee must have known all about them, at least by 1920 when he gave us his mature judgment on the nature of heterothallism, and specifically insisted that heterothallism can never be recognized by a morphological study alone. The writer (**1927**) stretched the point considerably when he stated that we should call those species of *Dioicomyces,* for example, heterothallic and not dioecious. Thaxter (**1931**) adopted this suggestion. In his table of contents he listed the genera to be treated under "heterothallic" and "homothallic." Discussing *Apatomyces* (p. 79) he used the expression "unisexuality or heterothallism." Today it would seem to the writer to be more in accord with Blakeslee's definitions to refer to Thaxter's "dioecious" species as haplodioecious and not as heterothallic, and to his "monoecious" species as haplomonoecious and not as homothallic. Thaxter fully recognized that haplodioecious differences might well be a provision for preventing self-fertilization. He also pointed out that cross fertilizations in "monoecious" species may very well be the more frequent because the antheridia mature earlier than the carpogonia on the same plant. "Antherozoids" mature on the plant over long periods after its carpogonia have been fertilized. Haplodioecious red algae and Laboulbeniales species certainly could also be heterothallic in the Blakeslee sense, but no one has as yet proved this experimentally.

We have in *Ascobolus magnificus* (Dodge, **1920**) a species which may possibly be both haplodioecious as well as heterothallic. Thalli from single ascospores produce neither ascogonia nor antheridia when grown separately. It is only when two thalli of opposite sex-reaction are grown together that very striking ascogonia and antheridia develop. They are, however, always formed on *different* hyphal branches. Shear and Dodge (**1927**) discussing this *Ascobolus* say: "In all probability the gametophytes come to maturity and produce reproductive structures only when grown together in the same medium, the mycelium of each sex so changing the nature of the medium as to stimulate the development of the reproductive structures on the mycelium of the opposite sex." We know that *Ascobolus magnificus* is heterothallic but we do not know whether it is haplomonoecious or haplodioecious.

Raper (**1940**, **1942**) has described some highly interesting experiments with species of *Achlya,* which when fully supplemented with genetic experiments will really show how complicated can be the questions of sex, sexuality, phenotypic sex cell-differentiations, heterothallism, haplodioecism, homothallism and haplomonoecism. Those who seek to explain everything relating to sex in the fungi by some simple formula should read Raper's very illuminating papers. He has shown, first of all, that there must be factors, no doubt heritable and segregated at meiosis, which govern the synthesis of sex stuffs, just as must be the case with *Ascobolus magnificus.* In both instances the effects of these sex hormones are manifested by the development of sex organs. It is not clear, however, whether or not other heritable factors in addition to those readily manifested, are a necessary adjunct. Are heterothallism and haplodioecism synonymous in *Achlya?* Are those sex factors which determine the +/− relations ever the same ones that govern the differentiation of the ♀ and ♂ sex organs? We must await adequate genetic work on such forms as *Ascobolus magnificus* and the species of *Achlya* before these questions can be settled. Raper, in his discussions, appears to be cognizant of the complexity of the situation as he does not make too many sweeping statements one way or another. We are not quite clear, however, as to his latest views on what constitutes heterothallism in *Achlya bisexualis* and *A. ambisexualis.* In the syntheses of sex stuffs by races of opposite mating types, *Achlya* and the species of *Chlamydomonas* worked on by Moewus (**1938**) have something very important in common.

Species of *Neurospora* (Shear and Dodge, **1927**), *Sclerotinia gladioli* (Drayton, **1932**) and *Bombardia lunata* (Zickler, **1934**) are excellent examples of heterothallic species of the sort in which, theoretically at least, mycelia from single ascospores often produce both incipient ascocarps and spermatia. They are of the class which we should refer to as normally haplomonoecious *and* heterothallic. The fact that certain races fail to produce ascogonia or other receptive structures, and that other races fail to produce spermatia, does not alter the fact that production of ascocarps by heterothallic species is regulated first of all by pairs of factors primarily concerned with sex-reactions or mating type differences such as Blakeslee would characterize as +/− relationships.

Aronescu (**1933**) found a rather well-marked segregation of factors controlling the development of incipient perithecia. When a certain pair of albinistic races of *Neurospora sitophila* were crossed, four of the progeny races from single asci developed large numbers of "sclerotia" (incipient perithecia). These cultures were dark grayish in appearance. The other four f_1 races produced few if any incipient perithecial primordia; on Czapek's medium no incipient perithecia were formed. To be on the safe side she concluded merely that while she obtained a clear cut segregation of factors controlling abundance and paucity of perithecial primordia, one should interpret her results as showing merely that some races are capable of greater fructification than others as indicated by their numbers of receptive bodies.

Zickler (**1934**) reported important genetic work on *Bombardia lunata.* His figures of ascogonia and spermatangia with spermatia leave little to be desired as proving that normally a mycelium from a single ascospore is haplomonoecious. The species is also strictly heterothallic. He refers to the two kinds of thalli as *A* & *a* reaction groups. Among other things he found both *A* races and *a* races of *"bulbosa,"* both normally producing a great many incipient perithecia and also spermatia. Another race, *"lanata,"* produced few if any incipient perithecia although this race always produced many spermatia. Segregations were such that he obtained *"lan"* races which were of opposite sex-reaction types, *A-lan* and *a-lan.* Now when he attempted to intercross these four races by the spermatization method he obtained the results which were indicated in his diagram. The solid lines indicate positive reactions resulting in normal perithecia; broken lines indicate failure.

It is self-evident that if a mycelium does not develop perithecial primordia or receptive structures, either by itself or under the stimulus of spermatization or of sex-hormones, it can not be made to fructify. Zickler says that from his diagram one might get the impression that he had here something comparable to the tetrapolar type of segregation such as prevails in certain higher basidiomycetes. This he says is not the case, however.

(To be concluded)

NOTES AND BRIEF ARTICLES

Common Names May Be Highly Important

One is accustomed to think of common names as merely incidental, to be changed at will. Not so with the common names of poisonous plants, however. A single instance will illustrate what I mean.

Krieger did an excellent job in his "Guide to Mushrooms." There is almost nothing to criticize in all the fact-filled 500 pages. But in selecting a common name for *Amanita verna* he translated the Latin and used "Spring Amanita," a procedure followed in thousands of cases and ordinarily perfectly legitimate. Then he came to *A. virosa,* which had no common name, so he called it "Destroying Angel." It is white, it is deadly—what's wrong with the name? Simply this; it belongs to another plant (*A. verna*) and the arbitrary change, while perfectly innocent, might lead to endless confusion and possibly serious consequences.

W. A. Murrill

A New Name

Since the generic name *Longia* has already been applied to a genus of rusts by Sydow [1] the use of the same name for a genus in the Gasteromycetes is untenable.[2] The generic name **Longula** gen. nov. will therefore apply to this genus of Gasteromycetes and the combinations will be **Longula texensis** (Berk. & Curt.) Zeller comb. nov., and **L. texensis** var. **major** Zeller comb. nov.

S. M. Zeller

A Simple Method for Preparing Corn Meal Agar

In identifying various yeast-like fungi isolated from human sources, one has recourse to the use of corn meal agar.

[1] Ann. Myc. **19**: 165. 1921.
[2] Zeller, S. M. Mycologia **35**: 414–417. 1943.

The usual methods cited for the preparation of this agar call for several filtrations through paper and cotton. These operations are quite tedious. With the use of a "Silex" type coffee pot fitted with a "Cory glass filter rod," it has been found practicable to prepare the agar in less time and with greater simplicity.

The technique is the same used in brewing coffee except that 40 gm. of yellow corn meal are used in place of the ground coffee and 500 ml. of distilled water in place of tap water. The water is then heated and passed and repassed through the corn meal not once but at least eight times. At the end of this procedure, the volume of the extract is measured, brought back to 500 ml., and the extract then added to a two liter flask containing 15 gm. of agar and 500 ml. of distilled water. The flask is plugged and autoclaved for 15 minutes at 15 pounds pressure. Plates can then be poured and stored away till needed.

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THE RELATION BETWEEN VERMICULARIA GRAMINICOLA WEST. REPORTED ON SUGARCANE AND PHYSALOSPORA TUCUMANENSIS SPEG.

In 1896 C. Spegazzini [1] reported *Vermicularia graminicola* West. as occurring upon sugarcane leaves (*Saccharum officinarum*) in Argentina. Material of this was obtained from Juan C. Lindquist of the "Instituto Spegazzini," La Plata, labeled "No. 6750." After careful microscopic examination of this material, it was found that it contained two different types of fruit bodies, acervuli and perithecia. The conidial stage represented by the acervuli (conidia, setae, and appressoria) fit the description of *Colletotrichum falcatum* Went, while the perithecial or ascosporic stage was typical of *Physalospora tucumanensis* Speg.

The conidial and perithecial stages found in Spegazzini's material agreed reasonably well with those of the red rot fungus of

[1] Spegazzini, C. Hongos de la cana de azucar. Rev. Fac. Agron. y Vet. **2**: *227–258*. 1896.

sugarcane as studied by the writer [2] in Louisiana. Therefore, it is considered that Spegazzini's specimen of *Vermicularia graminicola* is cospecific with *Physalospora tucumanensis*. This Argentinian material has been kept in the herbarium of the Botany Department at Louisiana State University, Baton Rouge, Louisiana, under the number 4667 as *Physalospora tucumanensis* Speg.

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SELENOPHOMA ON GRASSES, II [1]

Maire (Bul. Soc. Bot. Fr. **53**: CLXXXVII. 1906) described the genus *Selenophoma* as follows:

> "*Conceptaculis immersis, erumpentibus vel subsuperficialibus, ostiolo punctiformi plus minusve papillato, membranaceis, nigris; sporis* Vermiculariae *quasi curvatis et utrinque acutis, muticis, hyalinis; sporophoris brevissimis simplicibus.*"

This genus is hereby emended to include also species with somewhat obtusely pointed spores, other characters agreeing. With this emendation, the following new species is described.

Selenophoma obtusa sp. nov.

Maculis fulvellis, margine fusco v. lavendulo; pycnidiis globosis, nigris, 40–150 × 40–138 μ; pycnophoris cuspidatis, prominulis, 3–7 × 2–3.5 μ; pycnosporulis curvatis, utrinque obtusis v. sub-acutis, 13–17 × 2.5–4.2 μ. Hab. in foliis et culmis vivis *Sitanii hystricis*, Mt. Shasta, Calif. (typus), *S. Hanseni, Stipae Richardsonii, Poae aridae, Elymi glauci, E. condensati*, et *Agropyri inermis* in America Boreali occidentali.

[2] Carvajal, Fernando & Edgerton, C. W. The perfect stage of *Colletotrichum falcatum*. Phytopath. **34**: 206–213. 1944.

[1] (Selenophoma on Grasses, [I], Mycologia **32**: 415. 1940.) Coöperative investigations between the Divisions of Cereal Crops and Diseases, Forage Crops and Diseases and Dry Land Agriculture, Bureau of Plant Industry, Soils, and Agricultural Engineering; and Nursery Division, Soil Conservation Service, U. S. Department of Agriculture and the Oregon and North Dakota Agriculture Experiment Stations.

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It is proposed also that *Phyllosticta stomaticola* Baüml. be included in *Selenophoma Donacis* (Pass.) Sprague and A. G. Johnson as **S. Donacis** var. **stomaticola** (Baüml.) comb. nov. Also that *Septoria Everhartii* Sacc. & Syd. be transferred to the genus *Selenophoma* as **S. Everhartii** (Sacc. & Syd.) comb. nov.

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